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**16.—A Review of Australian Fossil Marsupials**

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**Introduction**

In recent years there has been a great resurgence of interest in Australian marsupials. In the case of the modern mammals this has produced a vast body of information through the application of modern physiological and ecological techniques, knowledge which is now replacing the natural history anecdotes and zoological inferences of past generations. In a similar fashion, the advent of the four-wheel drive vehicle, of plastics, and the discovery of new techniques for handling data, have produced encouraging signs that knowledge of fossil marsupials is also likely to increase. Today, palaeontological field-work aimed at the discovery of new fossil marsupials in Australia is going on from most of the Australian museums and also,

with spectacular success, from several American universities. Unfortunately, as yet, only a small fraction of the results of this new work has been published.

Despite our present-day activity and the publications of our predecessors, our knowledge of pre-Pleistocene marsupials remains small because descriptions are, as yet, available of only very few Tertiary fossils and of these only one (*Wynyardia*) is certainly older than Miocene. Preliminary descriptions have been published of some of the recently discovered middle and upper Tertiary forms from Central Australia (Stirton 1955, 1957a), while stratigraphic information from a number of sources is also being made available (Stirton, Tedford & Miller 1961, Ludbrook 1963, 1963a, Balme 1963). When the full descriptions, proper comparisons, and the ages of these fossils are known they will provide the first real framework for palaeontological studies on the Age of Marsupials in Australia.

Although there are great numbers of Pleistocene fossil marsupials in the Australian Museums, little has been done with them since they were originally described. Thus, advances in the knowledge of the anatomy and classification of recent forms, and concepts of population biology and of faunistics, have played little part in their interpretation. In addition, most of the early workers did not recognise the need for accurate stratigraphic localization. Thus, it is scarcely surprising that one of the most pressing tasks in Australian Palaeontology today is that of rediscovering the classic localities, and localizing the old material through comparison with new. It is only in this way that the species names in use can be stratigraphically allocated, and it is only through these new collections that ranges of morphological variation of the various species will be determined. At present "species" are often represented by samples which may not be stratigraphically homogeneous and population studies based upon them may be quite erroneous. An outstanding example of such work has been the studies of Woods (1960a), and more recently of Bartholomai (1962, 1963), on the Darling Downs faunas. Woods has shown that this material, which was formerly regarded as a single rather mixed unit, belongs to two distinct,

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successional faunas. Although physical superposition has not yet been demonstrated, these are probably Upper Pliocene and Lower (or Mid) Pleistocene.

Such work, if it is to be done to modern standards, is very slow and it is fortunate that (even omitting the numbers of overseas workers) there are in Australia today almost as many active researchers in this field as there have been in the whole of our history.

The review which I present here is a general one of the outlines of our knowledge of Australian fossil marsupials to date. However, in it I also take the opportunity to give fresh data and conclusions relative to a number of fossils which I have studied but have not yet published upon. These are *Glaucodon ballaratensis*, the *Thylacinus* complex, the Grange Burn "cuscus" (which is not a cuscus but a potoroo), and *Wynyardia bassiana*. I also propose a new ordinal classification of the Marsupialia to bring their arrangement more into line with that accepted for the Eutheria. I also consider the current status of the Continental Drift hypothesis and conclude that it provides an adequate explanation for anomalies in the composition of the Australian mammalian fauna.

### Classification

Today, marsupials occurring in Australia are usually classified into three major groups. These, following Simpson's (1930) example, are conventionally given the rank of Superfamilies, as are the three other major taxa of marsupials which occur in Palæarctic and Neotropical regions (see also Simpson 1945). This rather low rank for each of these groups fits well with the traditional practice of regarding the Marsupialia as a single Order of Mammalia, but it also implies an unwarranted degree of homogeneity in a group of animals which have evolved for just as long as the Eutheria have; by contrast these are currently subdivided into twenty-six Orders.

Fossil marsupials, particularly those of the Australian Pleistocene, clearly demonstrate a wide variety of forms which, if they had been eutherian, would have been distributed among several orders. Thus, if the kangaroos and wallabies are antelope- and deer-like, the sthenurines bovid-like and the diprotodontids hippo-like then the native cats can only represent some such unspecialized Carnivora as the civets and mongooses. The bandicoots are very different again from both of these groups and clearly invite comparison with yet another order.

This idea is not anything original for taxonomists have long recognized this inconsistency in classification. For example, Cain (1959, p. 214) has said in explanation: "Because of their peculiar features [marsupials] are always ranked as a single order of mammals within a separate class, although the briefest inspection is enough to show that there is at least as much difference between a kangaroo and a dasyure (for example) as between an insectivore and a rodent, let alone a rodent and a lagomorph. Because eutherian mammals were the first to become familiar to the anatomists of the western world, and even more because our species belongs to them, they have been taken as normal and the extraordinary

'abnormality' of the marsupial urinogenital system has sufficed to keep marsupials as a single order. Had we known the marsupials first and especially if we had belonged to them, they would have been classified in several orders, and no doubt the 'abnormality' of the eutherian genitalia would have sufficed to keep the number of eutherian orders much lower than at present."

In the classification which follows I do not discard the six superfamilies but, in order to emphasize the breadth of the whole radiation, and since I believe that a synthetic view of palæontology and neontology requires it, I group these further.

In an earlier review of the beginnings of the marsupials and of the main features of their phylogeny (Ride 1962) I had pointed out that marsupials had formerly been grouped in two higher taxa (suborders) and the abandonment of these by Simpson in 1930 was one of the most important advances in marsupial classification of our time. Through discarding them Simpson promoted a freer mental approach to problems of interrelationship within the marsupials as a whole. The problem which now arises is whether or not a new ordinal classification would have the same restrictive effect as did the subordinal classifications attributed to Owen and Bensley (or de Blainville). I think that this is unlikely because it cuts across no phylogenetic divisions. It also raises no problems of intercontinental migration.

The earlier classifications raised problems in both of these directions.

Although Owen's classification into Polyprotodontia and Diprotodontia was not intended to be phylogenetic it became so in the minds of students and, when the cænolestoids were added to the Diprotodontia, argument inevitably became confused with the issue of Continental Drift. By contrast, Bensley's classification was phylogenetic but was complicated by his misinterpretation of the structure of the didelphoid foot (see Goodrich 1935), but better understanding today makes it possible that his *Syndactyla* will eventually be used as a "cohort" in future marsupial classifications. Both systems (as phylogenetic arrangements) had their proponents and the problems in the minds of students as to which was more likely to be correct were only disposed of by Simpson's action in abandoning them altogether. He rejected these "key-classifications" which were based on single characters and subdivided the Marsupialia into five or six groups of very different importance and variety but of equal or nearly equal antiquity.

In 1930 there seemed to be no good reason for grouping the superfamilies into taxa at higher level but, since then, fossils of about the right age (Palaeocene and Lower Eocene) and with suitable characters to provide a transitional stage between the non-Australian superfamilies Didelphoidea and Borhyaenoidea have been discovered (i.e. *Eobrasilia* Simpson 1947 and *Patene*-like forms Simpson 1948, p. 49). If the Dasyuroidea be added to these—and there is little to argue against this course in spite of the absence of transitional fossils between them and the South American superfamilies—then the argu-

ment that Dasyuroidea, Didelphoidea and Borhyaenoidea form a single unit comparable with the eutherian Carnivora becomes even stronger. Most authors regard the modern Dasyuroidea as not very greatly modified descendants of the original didelphoid invaders of Australia and, since the Phalangeroidea at least (and also the Perameloidea) warrant ordinal status by comparison with Eutheria, I take the formal step of proposing four orders of Marsupialia.

The classification which I adopt is as follows:

Class MAMMALIA Linnaeus, 1758.

Infraclass METATHERIA Huxley, 1880.

Superorder MARSUPIALIA Illiger, 1811.

Order 1. MARSUPICARNIVORA *nov.*

Superfamilies

1. Didelphoidea : American Opossums etc., U. Cret—L. Mioc, Pleist—R, N. Amer.; Eoc-Mioc, Western Europe; Palaeoc—R, S. Amer.
2. ‡Borhyaenoidea : South American marsupial carnivores. Palaeoc-Plioc, S. Amer.
3. Dasyuroidea : Australian Native-cats etc. ?Mioc — R, Aust.; R, N. Guinea.

Families

- 1 Dasyuridae : ?Mioc — R, Aust.; R, N. Guinea.
- 2 Thylacinidae : U. Plioc — R, Aust.; ?Pleist, N. Guinea.

Order 2. PAUCITUBERCULATA\* Ameghino, 1894.

Families

1. Caenolestidae : Opossum rats etc., Palaeoc — R, S. Amer.
2. ‡Polydolopidae : Palaeoc — Eoc, S. Amer.

Order 3. PERAMELINA Gray, 1825.

Family

1. Peramelidae : Bandicoots, Plioc — R, Australia; R, N. Guinea.

Order 4. DIPROTODONTA Owen, 1866.

Families

1. Phalangeridae : Possums, cuscuses, marsupial lions, etc., ?Mioc — R, Aust.; R, N. Guinea.
2. ‡Wynyardiidae : Oligocene, Tasmania.
3. Vombatidae : Wombats. Pleist — R, Aust.
4. ‡Diprotodontidae : Mioc — R, Aust.; ?Plioc, N. Guinea.
5. Macropodidae : ?Mioc — R, Aust.; ?Plioc — R, N. Guinea.

Marsupialia *incertae sedis*

Family Notoryctidae : Marsupial Moles. R, Aust.

*Numbers of genera in orders.*—If the fossil and modern genera of these orders are counted and the generic concepts of a single conservative author are employed (G. G. Simpson 1945), they fall well within the range of magnitude of orders of Eutheria. Thus:

Marsupialia — Marsupicarnivora 64, Paucituberculata 21, Peramelina 5, Diprotodonta 48. *Incertae sedis* 1.

Eutheria (some orders only) — Embriothopoda 1, Tubulidentata 1 (possibly 2§), Dermoptera 3, Pholidota 1 (possibly 4§), Pyrotheria 4 (possibly 6§), Dinocerata 8, Astrapotheria 9, Hyracoidea 13, Sirenia 16, Proboscidea 24, Lagomorpha 33, Perissodactyla 158, Carnivora 377, Artiodactyla 419.

In making these comparisons, however, we must remember that we know little of the fossils of some of these marsupial orders and the values shown here for the numbers of genera included in each are not really comparable with those given for the eutherian orders because they are too low. This is made clear by comparing the approximate percentages of genera of marsupial and eutherian orders which are known only as fossils. Since a number of the smaller orders of Eutheria are known only as fossils, comparison has been limited here to those which, like the orders of Marsupialia, contain some living representatives. The percentages of genera known from fossils only in each order are:

Marsupialia — Marsupicarnivora 68%, Peramelina 0%, Paucituberculata 86%, Diprotodonta 35%.

Eutheria — Tubulidentata possibly 50%§, Dermoptera 67%, Pholidota possibly 75%§, Hyracoidea 77%, Sirenia 88%, Proboscidea 92%, Lagomorpha 70%, Perissodactyla 96%, Carnivora 70%, Artiodactyla 80%.

The same data reveal that our knowledge of non-Australian fossil marsupials is comparable with that of eutherians but knowledge of the Australian forms lags far behind that of eutherian orders of comparable size. This is emphasized by the removal of the Australian component from Marsupicarnivora; this causes the value to rise to 80%, with 0% of purely fossil genera known within the Dasyuroidea||.

The marsupial orders do not match the eutherian orders only in numbers of genera but also in the breadth of their adaptive radiations. I have already made brief mention of similarities between Diprotodonta and Artiodactyla and, in general outline, a similar comparison can be drawn between Marsupicarnivora and Carnivora. In making such a comparison it must be first recognized that the total adaptive scope of the two orders is not directly overlapping. Thus, some ecological branches (like the Pinnipedia and some wholly vegetarian Procyonidae) of the

§ Figures qualified thus are obtained by including those genera which Simpson includes with reservation.

|| In these figures *Glaucodon* (Dasyuroidea) and *Ischnodon* (Peramelina) are not included because they were published after the date of Simpson's 1945 monograph from which the data are drawn. To insert these without adding newly described genera of Eutheria would be pointless.

\* I follow Cabrera 1919 in adopting Ameghino's name for this taxon and like him exclude *Microlestes* and *Hypsiprymnopsis* from the concept as well as the "Hypsiprymnoidae"—see Ameghino 1903 (Vol. 13, p. 962 of *Obras completas*).

‡ taxa comprising extinct forms only.

radiation of Carnivora are missing from Marsupicarnivora, but the Marsupicarnivora is widened in other directions through including many of the equivalents of the eutherian order Insectivora within it; these are excluded from Carnivora. Otherwise, remarkable similarities exist between the taxa. Relatively unspecialized carnivores approaching Mustelidae and Viverridae are found in Borhyaenoidae (*Amphiproiverra*) and Dasyuroidea (*Dasyurus*), and omnivorous animals like the marsupials *Didelphis* and *Philander* can be equated with members of the Raccoon family (Procyonidae, e.g. *Bassariscus*). *Sarcophilus*, the Tasmanian Devil, is like a Wolverine (*Gulo*) or a Hyaena in its carnivorous specializations and *Thylacinus* is like a wolf. *Chironectes* (the Water Opossum) with its slightly flattened tail and webbed toes might even be regarded as an early approach to otter-like form. One of the most remarkable ecological and functional similarities is that between *Thylacosmilus* the Marsupial Sabre-tooth (Pliocene, South America) and *Smilodon* and the other true sabre-tooth tigers (see Simpson 1941a). As far as I know there is no direct equivalent between marsupials and such highly specialized herbivorous carnivores as the procyonids *Potos* (the Kinkajou) and *Ailuropoda* (the Giant Panda) but, as already mentioned, this is only to be expected when broad comparisons are being drawn between orders.

The insectivore-like forms among the Marsupicarnivora include Didelphoidea: *Peratherium*, Eocene-Miocene Europe, North America; *Marmosa*\*, mouse-opossums, Recent South America; and Dasyuroidea: *Sminthopsis*, *Planigale* and *Antechinus*, Marsupial-mice, Recent

\* Information on the dietary preferences of South American mammals referred to in this review is from Hall & Dalquest 1963.

and Pleistocene, Australia. Some of these are arboreal, e.g. *Marmosa* and *Caluromys* of South America, and *Phascogale* (*sens. strict.*) of Australia. This latter genus should possibly be equated with the tree-shrews *Tupaia*. If *Notoryctes* (the Marsupial Mole) should prove to be a dasyuroid its only equivalent is also in the Insectivora (i.e. *Talpa* or *Chrysochloris*).

Finally, the taxa have comparable ranges in time: Carnivora occurred from the L. Palaeocene to Recent, and Marsupicarnivora from the U. Cretaceous to Recent.

## PHYLOGENY

Lacking fossils we can only derive the probable relationships of the Australian marsupial orders by inference from the characters of their modern representatives. Such a phylogenetic tree is shown in fig. 1. This is essentially the same as that shown in my 1959 review of some problems of marsupial phylogeny (Ride 1962) but incorporates the ordinal classification given here. It illustrates the conclusion that the major groups of marsupials may be arranged as a series of structural grades. Recently Masai (1960) and Dillon (1963) have published results which threw some doubt on the position at which duplicommissurally (i.e. the possession of a fasciculus aberrans in the forebrain) should first appear in this dendrogram. Their results are so at variance with those of earlier workers, such as Elliot Smith and A. A. Abbie, that I have not taken them into account and it is quite clear that further examination of specimens of the various species must be made in case the apparent disagreement is produced by differences in technique, in interpretation, or even through faulty material.

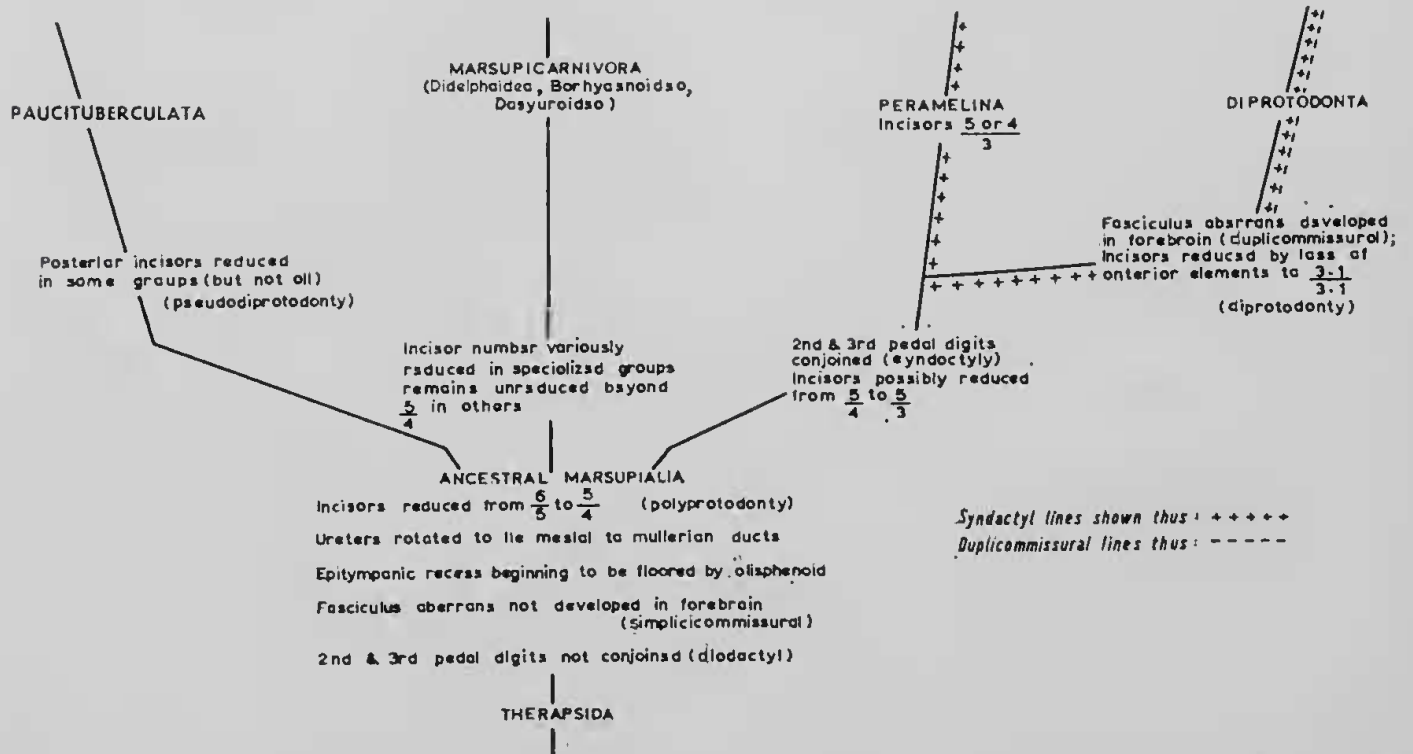


Fig. 1.—The sequence of morphological differentiation in the evolution of marsupial orders (modified from Ride 1962).

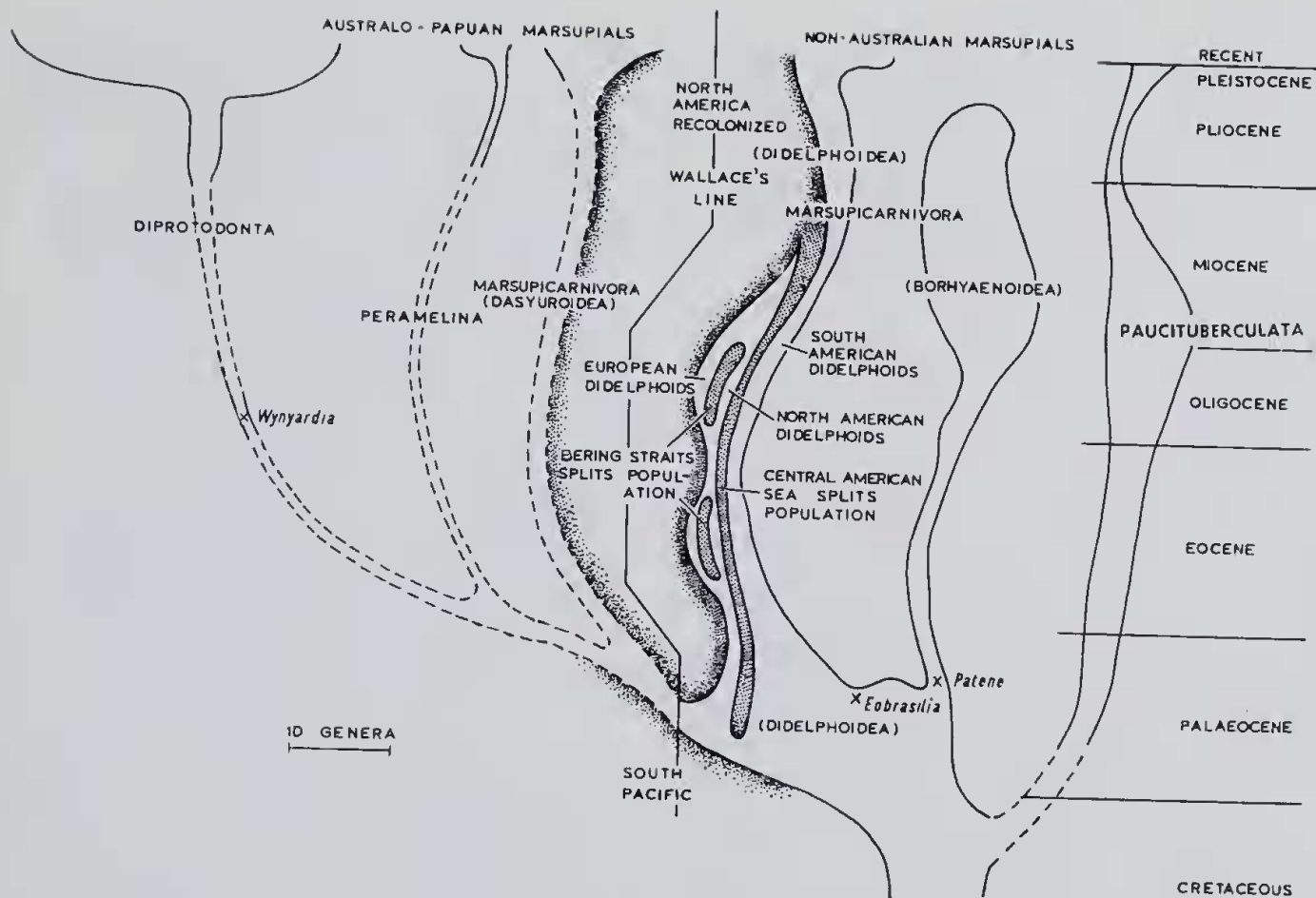


Fig. 2.—A family tree of marsupials. Horizontal distances between unbroken lines limiting phyla represent known numbers of genera. Stipple represents aquatic barriers (modified from Ride 1962).

If the results of Masai and Dillon were to be confirmed, they would produce no change in the general phyletic outline but they would have the result of pushing the evolutionary origin of the fasciculus aberrans into the various lines within the already evolved Diprotodonta, since some of these will be like all other marsupials in lacking it while most will possess it. However, Masai states that some Diprotodonta possess a corpus callosum. If this is so, they differ from all other marsupials and resemble Eutheria—a somewhat remarkable state of affairs.

The widely held view of the fundamental dichotomy between marsupial and eutherian female urinogenital systems has been challenged by Kean (1961). He holds that the median (eutherian) vagina has become reduced in the marsupial line, following the reduction in size of the neonatus, and lateral vaginae have evolved as neomorph seminal ducts. It is Kean's view that embryological evidence is equivocal.

Figure 2 is a graphic summary of geographical and temporal distributions combined with the dendrogram of Fig. 1. Horizontal breadths of the ascending phyla represent the known numbers of genera at each horizon, and the diagram gives some indication of marine barriers to dispersal. However, it takes no account of the possible role of the Tethys sea as a barrier to dispersal from northern to southern Eurasia and leaves the question unanswered as to whether

marsupials entered Australia by means of a southern intercontinental connection or across Wallace's Line.

### MARSUPICARNIVORA

The fossil evidence of relationship between the two main groups of American Marsupicarnivora (the Didelphoidea and Borhyaenoidea) lies in the fossils *Eobrasilia*, *Patene* and a problematical group of five isolated molars of which Simpson (1948, p. 49) says: "These various teeth appear to represent a morphological group of fairly unified nature and intermediate in its (admittedly too few) known characters between borhyaenids and didelphids. The isolated teeth could be referred to either family. Among the Borhyaenidae they would be the most primitive known forms, among the Didelphidae the most advanced in the borhyaenid (or predaceous) direction. On the whole, I think them somewhat closer to borhyaenids, but they are almost perfectly intermediate as far as they go. In conjunction with the almost equally primitive *Patene*, they give a clue, slender but real, to the ancestry of the Borhyaenidae."

Simpson sums up his attitude (1948, p. 40) to the relationship of didelphids, dasyuroids and borhyaenids by saying: "Traced as far as possible to its fundamentals, the structure of borhyaenids in general seems clearly derivable from a primitive stock certainly pre-thylacinid and comparable only to the didelphids and the most primi-

tive dasyurids. It resembles both these stocks (which are very similar in essentials), and there is no conclusive evidence of relations to one or the other. Adaptively the group parallels the dasyuroids, but its inferred structural ancestry appears rather more didelphoid. The most probable conclusion is that in the Upper Cretaceous the didelphoids and dasyuroids had a common ancestry sharing the primitive characters of both groups, somewhat more like the Didelphidae than the Dasyuridae as we know them because the former are more conservative. From this stock the borhyaenids arose. They may very well have arisen from a carnivorous line progressing in the direction of the Dasyuridae, but not very far along this line, and surely before it had acquired its most characteristic specializations."

Of course, there are no fossil intermediates between dasyuroids and the American forms but comparison of the characters of even modern Dasyuroidea with Didelphoidea and Borhyaenoidea reveal no differences which separate them unequivocally.

Modern dasyuroids differ principally from didelphoids in that they are specialized in a carnivorous (or insectivorous) predaceous direction and are primarily cursorial. Thus Dasyuridae seldom possess the opposable hallux of the scansorial didelphoids and in this they resemble some Borhyaenidae (see *Prothylacinus* in Sinclair 1906, p. 371 and pl. 54) but not all. Whether the dasyuroid foot with its small and non-fully-opposable (and often very reduced) hallux and its frequently high degree of terrestrial specialization is more primitive than the highly specialized arboreal form of the didelphoid foot is not known. I know of no description of the hallux of a mesozoic mammal and I consider that Bensley's (1903, p. 163) view that the terrestrial foot of dasyuroid marsupials is secondly derived from the arboreal one is no more than an assumption. Bensley's belief is derived from Dollo's statements (1899, 1900) and from Bensley's own observation (p. 191) that the didelphoid *Marmosa*, which has an opposable hallux, meets the requirements of a prototype for the entire Australia marsupial radiation because it possesses "an indication of the syndactylous condition of the Phalangeridae". His conviction that this approach to *Marmosa* was reasonable was strengthened for him by the presence of the "primitive" five external styler cusps on the upper molars of the same genus. Goodrich (1935) has shown that his statement regarding syndactyly in *Marmosa* is erroneous. Bensley also pointed out that the dasyuroids differ from didelphoids in incisor number; dasyuroids never possessing more than 4/3. However, this statement is only true in relation to modern didelphoids since some (e.g. *Eodelphis cutleri*, Cretaceous, Belly River Fm., Canada, Simpson 1929, p. 128) have also reduced their lower incisors to three. Borhyaenidae reduce their lower incisors even further; thus *Borhyaena excavata* and *B. tuberculata* have an incisor formula of 3/2 while *Thylacosmilus* possesses none at all.

The molars of most modern dasyuroids differ from those of most didelphoids in that they lack the full complement of external styler

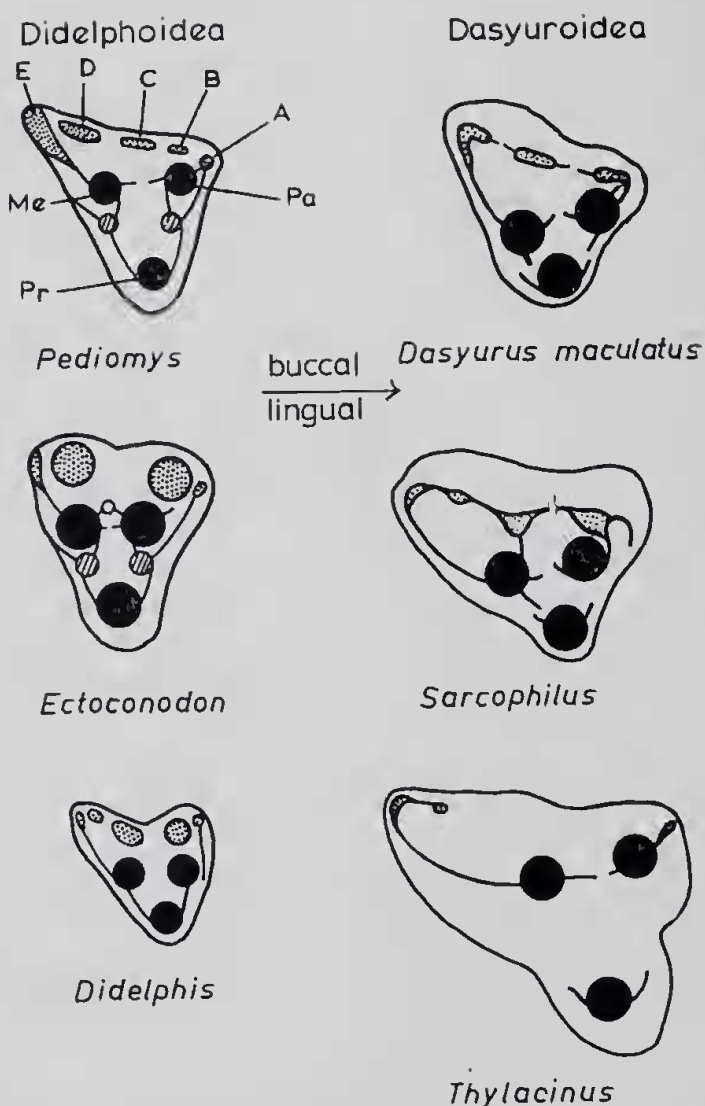


Fig. 3.—The cusps (black circles) and styler cusps (stipple) of the upper molars of Didelphoidea and Dasyuroidea. (Didelphoids after Simpson 1929, p. 119; dasyuroid second upper molars in collection W. Aust. Mus.)

cusps which Simpson has shown (from a study of very numerous Cretaceous didelphid upper molars as well as that of a large series of later didelphids from all known horizons; Simpson 1929, p. 119) is ancestral in the Didelphoidea—see fig. 3. These cusps vary considerably but Simpson says that, in teeth of the didelphid type, styler cusp A is always present and is only slightly external to the paracone save on  $M^4$ . B is never well developed, while C and D are about equally developed and usually form ridge-like crests parallel to the outer border. E is always present except on  $M^4$ . In modern Dasyuroidea there are seldom more than three styler cusps present. However, in Borhyaenoidea although the earliest forms possess the full complement of styler cusps (e.g. the five *Patene*-like molars illustrated in Simpson 1948, p. 49) more specialized forms have progressively fewer, *Patene* and *Procladosictis* (Palaeocene and Eocene) having only twin styles opposite the paracone and metacone and *Amphiproviverra*, *Prothylacinus* and *Borhyaena* (Miocene) having only a single anteroexternal styler cusp (Sinclair 1906). In *Thylacosmilus* (Pliocene) they are

absent (Simpson 1941). The lack of a full complement of styler cusps can thus scarcely be said to be a dasyurid character.

It is unfortunate that very little detailed descriptive comparative work has been published on the epitympanic region of marsupials since it seems likely that this structure may prove to be a better indication of separate phyletic lines in the Marsupicarnivora than the dentition. In Dasyuridae the epitympanic sinus anterior to the epitympanic recess is always ventrally enclosed in an alisphenoid bulla which grips the tympanic ring laterally (fig. 4). It is widely open into the epitympanic recess posteriorly. The dorsal and anterolateral part of

the epitympanic sinus is also greatly excavated into the substance of the alisphenoid and the squamosal where it may even penetrate into the root of the zygomatic arch dorsal to the glenoid. While the ear of *Thylacinus* is superficially rather different in appearance with its small flattened, and posteriorly incomplete, bulla and dorsally situated epitympanic sinuses, it is clearly derivable from that of the more typical dasyurid condition. In *Didelphis* (and in *Wynyardia* see p. 115) there is no dorsal or anterolateral "excavation" and the cavity (which probably represents the epitympanic recess alone) is only partly floored by an incomplete tympanic (or bullar) wing of the alisphenoid. Since the marsupials alone floor the epitympanic recess with the alisphenoid (Ride 1962) the uncomplicated condition seen in *Didelphis* is more likely to be primitive than the fully enclosed and "excavated" condition of Dasyurinae. Simpson's (1929, p. 129) illustration of the glenoid region of the Cretaceous didelphoid *Eodelphis*, while very incomplete, suggests a condition similar to that of *Didelphis*: the illustrations of Borhyaenoidea by Sinclair (1906) show yet another condition which may indicate that the structure will be useful in phylogenetic studies.

It seems that proper study of the Marsupicarnivora will reveal distinct lineages coming from a single basal stock but because Dasyuroidea on the one hand and Didelphoidea and Borhyaenoidea on the other are not far separate and subject to very similar pressures, and have been given equal ecological opportunities, a commonly-held mosaic of characters will persist giving rise to many examples of pairs of species in these different phyletic lines; pairs which more closely resemble each other than they do their less distantly separated relatives within their own lines. An example of this sort may well be the very strong resemblance between *Thylacinus* and Miocene Borhyaenidae, and it is probably also the reason for the result obtained by Wood (1924) who, when he compared forty-nine characters of Miocene Borhyaenidae, modern Dasyuroidea (including *Thylacinus*) and modern Didelphoidea, only obtained one "character" which unequivocally separated Dasyuroidea from the rest combined. This "character" was the location of dasyuroids in Australia while the other two superfamilies were confined to the Old World and the Americas (seventeen characters separated Didelphoidea from the other two, while five separated Borhyaenidae).

#### Australian Marsupicarnivora Superfamily Dasyuroidea

The native cats and their allies are a complex group. They are entirely Australo-Papuan and exhibit all grades of carnivorous specialization from those of the eaters of very small prey (e.g., insects and other arthropods, small mice and birds) like *Planigale* and *Sminthopsis* to those of highly specialized mammal killers and carrion feeders like *Sarcophilus* and *Thylacinus*. The transformation through the degrees of carnivorous specialization in normal members of the family takes place without reference to

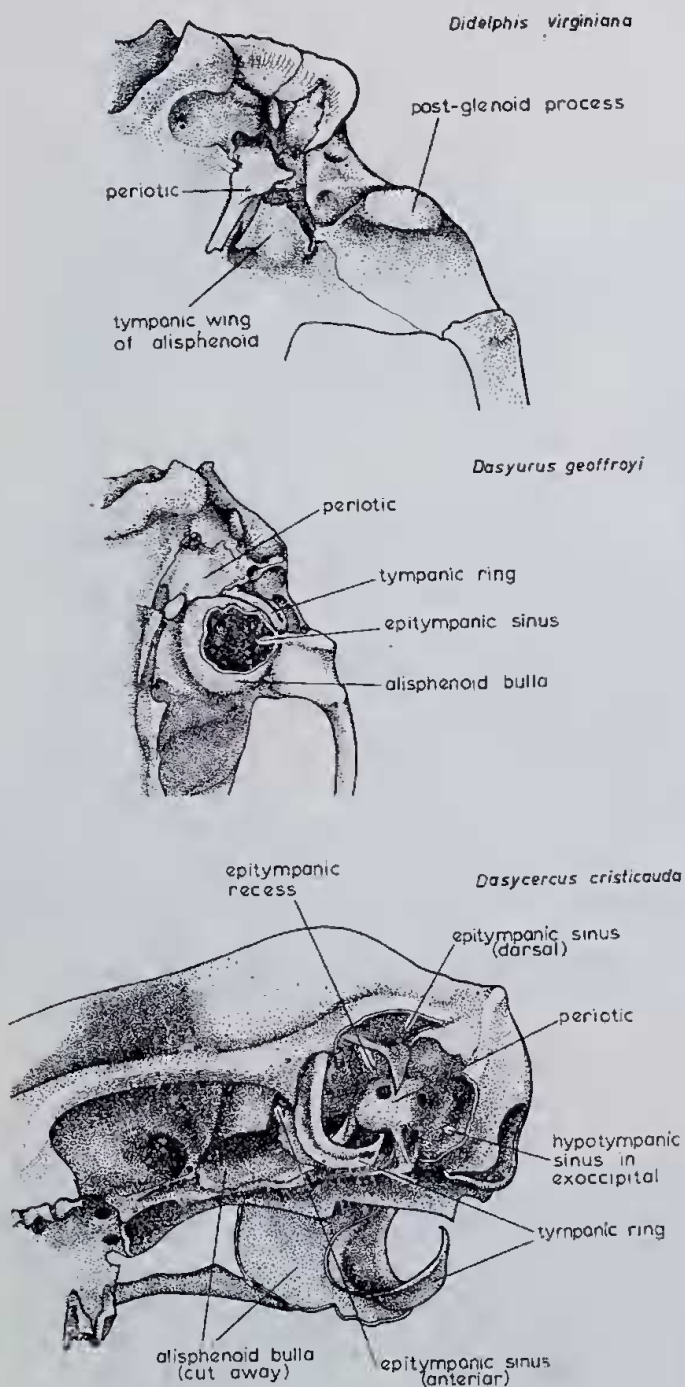


Fig. 4.—The epitympanic region of Marsupicarnivora. In both dasyuroids the alisphenoid bulla is cut away to reveal the epitympanic sinus. In *Dasyercus cristicauda* the squamosal and exoccipital are also cut away. The tympanic ring of the specimen of *Didelphis* has been lost. (Specimens in W. Aust. Mus.)

generic distinction and is closely connected with increase in the size of the body (Bensley 1903, p. 91). Among *Dasyuroidea* there are highly specialized forms which have become so modified that their immediate relationships are unknown. These are *Thylacinus*, the Tasmanian Wolf and *Myrmecobius* the Banded-anteater (termite-eater). These two genera are usually placed in separate major taxa from the others in a non-committal fashion; I employ Myrme-

cobiinae and Thylacinidae here in this manner. Their relative status as subfamily and family is entirely artificial and is adopted because, subjectively, the specializations of *Myrmecobius* for termite eating are more understandable as a development of typical dasyuroid structure than the obviously widely divergent yet parallel carnivorous specializations of *Thylacinus* which contrast strongly with those of *Sarcophilus* and other *Dasyuridae*. These paral-

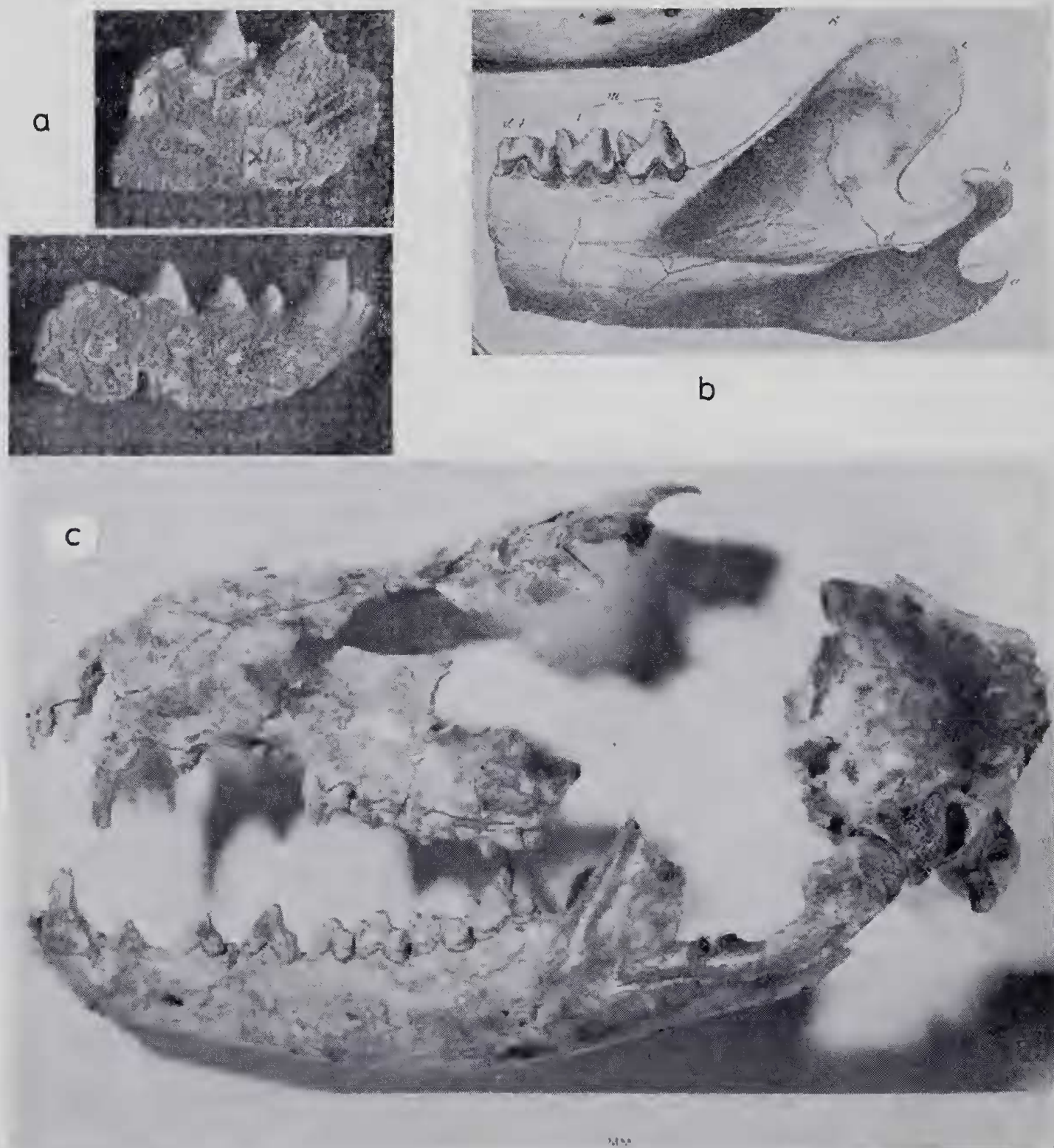


Fig. 5.—Type specimens of fossil *Thylacinus*. (a) Syntypes of *T. spelaeus* (Owen); Brit. Mus. (N.H.) Nos. Geol M10800, M10801. (b) *T. major* Owen; specimen unknown—fig. from Owen. (c) *T. rostralis* De Vis; Qd. Mus. No. F 730 (photograph by courtesy Qd Mus.). (a) and (c) to same scale; scale of (b) unknown.



lel specializations probably reveal an early divergence of two predaceous phyla within Dasyuroidea.

It might even be reasonable to give the Thyiacinidae superfamily rank and regard their relationship to Dasyuroidea as being the same as that between Didelphoidea and Borhyaenoidea. However, to date, only one genus and probably only one species is known and it seems best to leave things as they are until further material shows that the lineage of *Thylacinus* is as old and as diverse as that of the Borhyaenoidea. Stirton *et al* (1961) suggest that a specimen from the Etadunna Formation of central Australia (?Mioc, Ludbrook 1963a) may possibly be a dasyurid ancestor of Thyiacinidae and, if this should prove to be correct, family rank will probably be sufficient (but see p. 108).

### Thylacinidae Bonaparte, 1838

Only one genus of Thyiacinidae is known and the earliest specimen yet discovered came from the upper Pliocene Chinchilla Sand of the Darling Downs of Queensland. Today it is confined to Tasmania where the only living species (*T. cynocephalus*) is rare and possibly verges on extinction.

During the Pleistocene *Thylacinus* was widespread, occurring in Tasmania, continental Australia (where its remains are known from the fluvial *Diprotodon* Beds of the Darling Downs,

various cave deposits in Victoria, New South Wales, South Australia and in south-western Australia as far north as the Namban River), and even in New Guinea where a single mandible was found recently by Dr and Mrs R. Bulmer among pebble tools and flakes in an archaeological excavation near Kiowa in the Eastern Highlands (Van Deusen 1964).

Size, or proportional difference, has been the main criterion used by authors to differentiate the various described species of *Thylacinus*. Thus, *T. breviceps* (which is almost certainly a female and undoubtedly a juvenile specimen: Aust. Mus Sydney No. 774) was described by Krefft (1871) as a small species of modern Thylacine; and *T. spelaeus*\* of the Pleistocene was described by Owen (1845) as a larger species than *T. cynocephalus*, and *T. rostralis* likewise by De Vis (1894). De Vis claimed for his species that its proportions differed so much from those

\* The status of the name *T. major* Owen 1877 is uncertain. The species was figured (Foss. Mamm. Aust. Pl. V.) from the hinder part of a left mandibular ramus with M<sub>2</sub>, 3, 4. M<sub>3</sub> and M<sub>4</sub> are drawn as having very reduced talonids and are quite unlike those of *Thylacinus* while M<sub>2</sub> is an ordinary *Thylacinus* tooth. Lydekker (1887, p. 264) says that *T. major* was apparently given inadvertently for *T. spelaeus* and that the specimen illustrated by Owen was apparently drawn from the last three true molars of *Sarcophilus lanianus* added to the hinder part of a mandible of *T. cynocephalus*. I found no specimen of *Thylacinus* corresponding with Owen's figure in the collection of the British Museum (Nat. Hist.).

TABLE 1.

*Thylacinus*: Comparison of adult modern Tasmanian population with Western and Eastern (including specimens from New South Wales, Victoria and South Australia east of the Nullarbor) Cave-fossils

Ref. No.	Character	Block 1					Block 2					Block 3				
		Modern <i>Thylacinus cynocephalus</i>					Western cave-fossil <i>Thylacinus</i>					Eastern cave-fossil <i>Thylacinus</i> (= <i>spelaeus</i> )				
Morphological Name	$\bar{x}$	Observed range	n	s.	V	$\bar{x}$	Observed range	n	s	V	$\bar{x}$	Observed range	n	s	V	
	mm	mm		mm	mm	mm	mm		mm	mm	mm	mm		mm	mm	
1	M <sup>2</sup> pr.-me. ....	15.3	13.6-16.6	52	0.9	5.76	13.0	11.4-16.0	12	1.1	8.38	15.6	14.3-17.1	4	1.8	11.28
2	M <sup>3</sup> pr.-me. ....	17.8	16.0-19.7	46	1.2	6.50	15.4	13.2-17.6	9	1.1	7.41	17.6	15.8-20.2	3	2.3	13.20
3	M <sup>1-4</sup> length....	45.5	41.7-50.1	39	2.8	6.17	40.0	36.8-45.9	7	3.1	7.78	44.9	41.4-50.6	3	5.0	11.16
4	P <sub>4</sub> length ....	10.8	9.2-11.9	56	0.6	5.27	10.7	9.3-12.1	8	1.1	9.79	11.2	10.1-12.3	4	1.1	9.81
5	P <sub>4</sub> -C length....	49.4	41.1-59.4	47	4.3	8.76	49.9	38.0-57.9	4	9.1	18.20	52.6	50.9-54.3	2	2.4	4.58
6	M <sub>4</sub> length ....	15.7	13.9-17.1	46	1.0	6.20	14.9	12.8-16.9	8	1.4	9.46	16.5	14.4-18.6	4	2.0	12.42
7	Mand. Length	175	142-206	47	16	9.30	163	124-189	5	25	15.17	159	153-165	2	9.0	5.37
8	Ht. at P <sub>4</sub> ....	30.8	25.8-37.4	49	2.8	9.12	29.9	24.4-34.8	7	3.2	10.64	29.7	26.6-33.7	3	3.7	12.3

Ref. No.	Character	F		t Test			
		Variance Ratio		Comparison of Means			
Morphological Name	Between blocks 1 and 2 above	Between blocks 1 and 3 above	Between blocks 1 and 2 above		Between blocks 1 and 3 above		
			t	P	t	P	
1	M <sup>2</sup> pr.-me. ....	1.79	4.73**	8.1119	<0.01	0.6467	>0.5
2	M <sup>3</sup> pr.-me. ....	1.03	3.91*	5.94	<0.01	0.273	>0.5
3	M <sup>1-4</sup> length ...	1.23	3.18*	4.69	<0.01	0.338	>0.5
4	P <sub>4</sub> length ....	3.41**	3.70**	0.2471	>0.5	1.272	0.5-0.1
5	P <sub>4</sub> -C length ...	4.41**	3.23	0.1866	>0.5	0.9029	0.5-0.1
6	M <sub>4</sub> length ....	2.12	4.35**	1.9636	0.1-0.05	1.429	0.5-0.1
7	Mand. length ...	2.32	3.62	1.455	0.5-0.1	1.356	0.5-0.1
8	Ht. at P <sub>4</sub> ....	1.28	1.69	0.7802	0.5-0.1	0.6482	>0.5

\* Significant at 5% level.

\*\* Significant at 1% level.

TABLE 2.

*Thylacinus*: Sexual dimorphism in modern adult Tasmanian population

Ref. No.	Character	Block 1					Block 2					F	t Test	
		modern <i>Thylacinus</i> ♀					modern <i>Thylacinus</i> ♂						t	P
		$\bar{x}$ mm	Observed Range mm	n	s mm	V	$\bar{x}$ mm	Observed Range mm	n	s mm	V			
1	M <sup>2</sup> pr-me.	14.4	13.6-15.3	12	0.5	3.80	16.0	15.6-16.6	10	0.3	1.85	3.409*	8.092	<0.01
2	M <sup>3</sup> pr-me.	16.6	16.1-17.7	11	0.5	3.18	19.0	18.3-19.7	9	0.6	2.95	1.116	9.542	<0.01
3	M <sup>1,4</sup> length	42.6	41.7-44.1	9	0.8	1.82	48.1	46.3-50.1	9	1.3	2.71	0.283	10.878	<0.01
4	P <sub>1</sub> length	10.2	9.2-10.7	13	0.5	4.48	11.2	10.9-11.7	10	0.3	2.63	3.349*	6.467	<0.01
5	P <sub>1</sub> -C	46.5	41.5-50.9	11	2.6	5.53	53.6	51.7-55.0	8	1.3	2.5	3.674*	5.151	<0.01
6	M <sub>1</sub> length	14.8	13.9-16.2	9	0.7	4.59	16.4	15.1-17.0	9	0.6	3.67	1.276	7.825	<0.01
7	Mand. length	16.1	15.4-17.3	10	0.6	3.81	18.9	17.5-19.8	9	0.8	4.33	1.778	8.467	<0.01
8	Ht. at P <sub>1</sub>	28.7	26.7-29.9	11	1.0	3.45	33.2	31.1-36.0	9	1.6	4.77	2.561	7.107	<0.01

\* Significant at 5% level.

of *T. cynocephalus* that it probably also differed from *T. spelaeus* since Owen merely regarded this as a larger *Thylacine* than *T. cynocephalus*. De Vis said that both *T. rostralis* and *T. cynocephalus* occurred in the Chinchilla Sand.

The phenomenon of "gigantism" is as marked among the Australian Pleistocene forms as it is in other continental faunas and it has generally been believed that *Thylacinus* of the Pleistocene is an example of it. However, records of the presence of *T. cynocephalus* throughout these deposits is a complicating factor; furthermore, in recent years, collections of thylacines from the caves of south-western Australia have been made by the Speleological Group of the Western Australian Naturalists' Club (and in particular by D. L. Cook and R. Howlett, see Cook 1963, 1963a) and these have resulted in the discovery of further material of a very small thylacine of which fragments were first collected in the Mammoth Cave of Western Australia by L. Glauert in about 1909.

It is possible that these reputedly large and small thylacines are merely large and small individuals of a single species and in order to examine this I have, over a considerable period, collected data on thylacines from the British Museum (Nat. Hist.), the Oxford University Museum, the Australian Museum, the National Museum of Victoria, the South Australian Museum, the Queensland Museum, the Queen Victoria Museum Launceston, and the Western Australian Museum. In all, some sixty modern specimens which were collected in Tasmania have been measured in an attempt to gain an indication of the range of variation which might be expected in a fossil population of this genus. It is not possible to give more than a preliminary account of this study here, a study which is complicated by the fact that many specimens are mutilated (particularly the fossils) so that all characters measured are present in only a few individuals and, in the case of the fossils, very few even possess comparable characters. So far the work has been confined to the analysis of single characters but it is hoped ultimately to subject the data to multivariate methods. Here, in order to illustrate the conclusions to date, a selected group of eight separate characters is discussed (see Tables 1 and 2).

In *Thylacinus cynocephalus* variances are high. Coefficients of Variation (V) range from about 5-10 but there can be no doubt that only one species is involved in this single living Tasmanian population. The effects of growth have been eliminated as far as possible by selecting characters 1, 2, 3, 4, and 6 because these are dental characters taken on the enamel caps of permanent teeth. In the case of characters 5, 7, and 8 these are certainly likely to be effected by growth since they all include bone, but even these only include measurements from individuals in which dental development is complete.

Excluding the material from the deposits of the Darling Downs, and also the New Guinea specimen, it seems reasonable to divide the remaining fossil specimens into two samples. One of these (Block 3, Table 1), that from the caves of New South Wales, Victoria and eastern South Australia includes the type specimens of *T. spelaeus* from the Wellington Caves, N.S.W. (Brit. Mus. (N.H.) Geol. Nos. M/10800 and M/10801; Fig. 5) while the other (Block 2) is from the caves of the south-west.

The problem of analysis of these samples is complicated by the fact that *Thylacinus cynocephalus* is strongly sexually dimorphic (Fig. 6a and Table 2) and the data have had to be examined to see whether the samples depart sufficiently from normality to render the use of statistical tests invalid when these are constructed on the assumption that they are drawn from populations with normal distributions. It is found that only in the case of mandibular length would there be any doubt about the validity of applying normal statistical procedures.

Tests of variance ratio between modern and fossil samples (Table 1) show significantly different variances. Since the modern population is undoubtedly of a single species, it is tempting to conclude that more than one taxon is included in each fossil sample and that this is responsible for the high variance. However, in the situation where strong sexual dimorphism occurs (and in particular where the sex ratio can be assumed to be 1:1, or close to it) the variance cannot be expected to decrease with sample size because both sexes are likely to be represented. Dr. R. D. Hughes, of the Australian

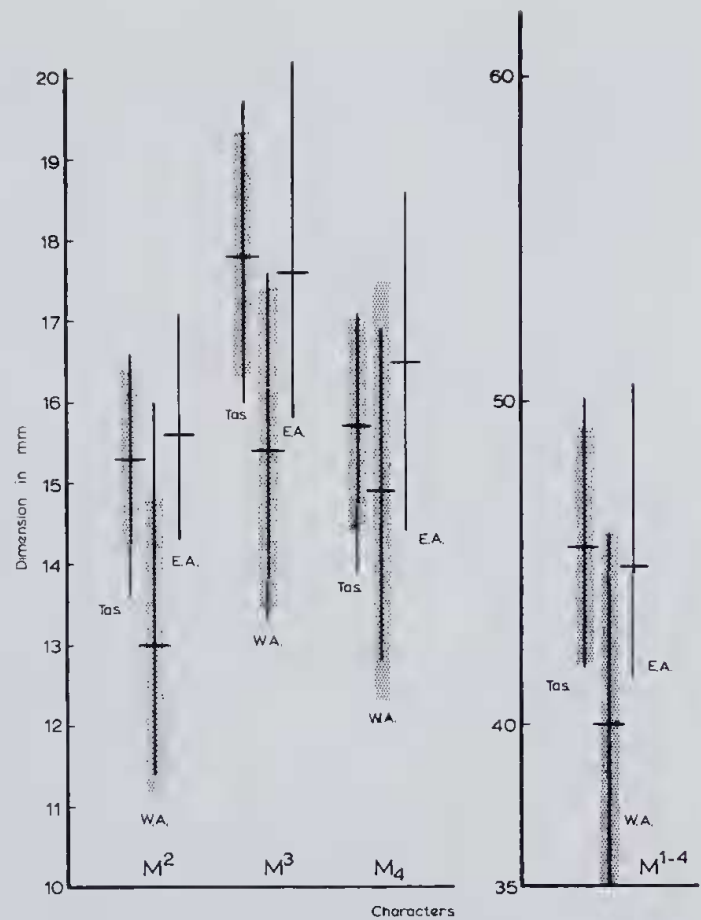
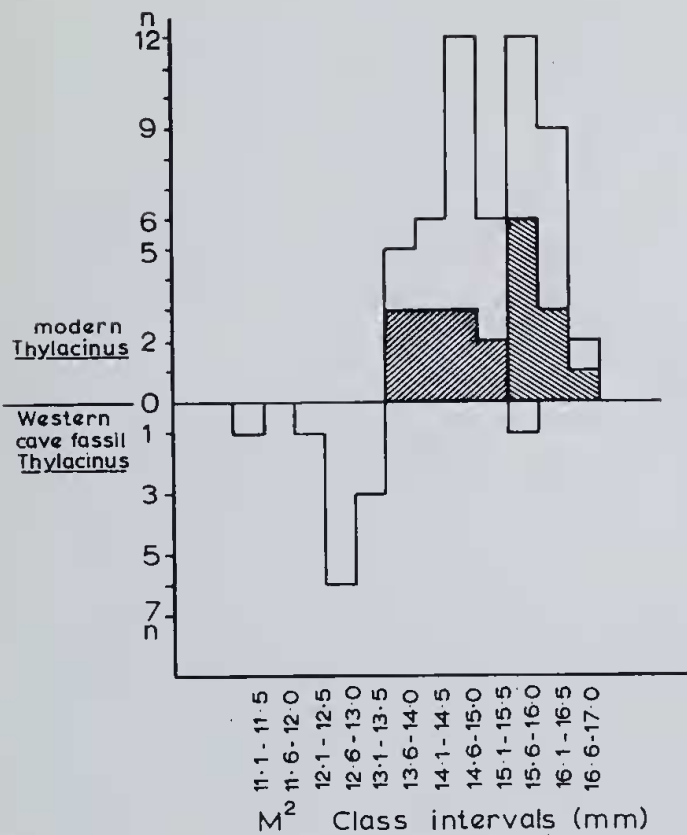
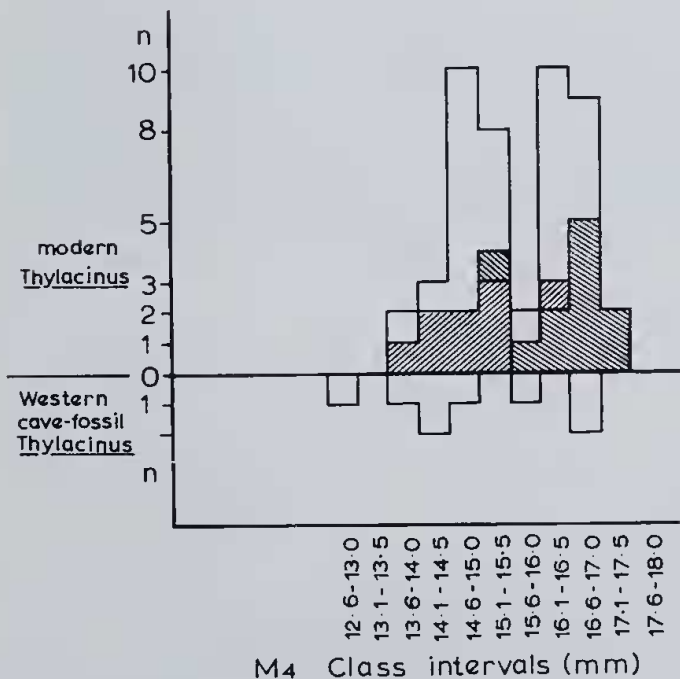


Fig. 6b.—Ranges of values of four characters of three populations of *Thylacinus*. Tas., Tasmanian modern; W.A., Western Cave-fossils; E.A., Eastern Cave-fossils. Vertical lines represent observed range. Horizontal lines represent sample means, stippled blocks superimposed upon Tas. and W.A. samples represent one standard deviation outside the confidence limits of the means.  $M^2, ^3$  are diagonal measurements across metacone and protocone,  $M_4$  and  $M^{1-4}$  are measurements of total antero-posterior length.






 ♀  
 ♂  
 NOT SEXED

Fig. 6a.—Histograms illustrating the distribution of classes of two characters of modern *Thylacinus* and Western Cave-fossil *Thylacinus*. Where sexes are known these are indicated by different shading.

National University, and I are examining this problem in greater detail and the results will be reported fully elsewhere, but, at present, we are of the opinion that the size of the variances in each of these small samples of fossils are those which might be expected in samples drawn from single species as exemplified by the much larger Tasmanian sample. We conclude that there is no longer any need to postulate sympatry between *T. cynocephalus* and *T. spelaeus* in the Pleistocene of eastern Australia.

Since individuals of *T. spelaeus* are supposed to be larger than those of *T. cynocephalus* their means should differ. Comparison of means by Student's *t* test (Blocks 1 and 3) shows no significant differences and it can only be concluded that, so far, this work does not support the separation of these two species.

Comparison between the means of *T. cynocephalus* and Western Cave thylacines reveals a different situation. Here *t* tests (between Blocks 1 and 2) are significant in characters 1, 2, 3 at the 1% level and approaches significance at the 5% level in character 6. All that now remains is to decide whether the difference is sufficient to warrant the use of a specific or subspecific name. Various approaches to this

kind of problem are possible (see Appendix) and it is sufficient to say that using a test which is compounded of the statistical discussions of the 75% Rule of Amadon and the 90% Rule of Mayr, Linsley and Usinger, the characters examined do not support separation even at a subspecific level at the present time (see Fig. 6b for a graphic representation of this). However, although recognition by name is not justified there is no doubt that in the Pleistocene of Western Australia there existed a population of *Thylacinus cynocephalus* which on an average contained smaller individuals than the modern form (and by inference its eastern Pleistocene representative).

The status of *T. rostralis* and the thylacines from the two Darling Downs faunas remains unsolved. The Holotype of *T. rostralis* (Queensland Museum F.730, Fig. 5) from Ellangowan nr. Cambooya in south-eastern Queensland is from the Pleistocene fluviatile deposits and lies at the upper end of the range of variation of *T. cynocephalus* (Character 1 of my Table 1 = 15.5, 2 = 17.9, 3 = 47.4, 4 = 12.0, 5 = 58.5, 6 = 17.1, 7 = 203, 8 = 38.9) and the only other specimens from the same beds (Queensland Museum F.3742 from King's Creek, Clifton, 4 = 14.1, 5 = 67.5, 8 = approximately 43; Brit. Mus. (N.H.) 35973 from Gowrie Creek, 1 = 17.1, 2 = 20.2) also have values that are very high. It is thus possible that *T. rostralis* is a distinct form. A value of 18.6 for a single isolated last lower molar (character 6) from the Pliocene Chinchilla Sand also suggests that this form may possibly be distinct as well.

The New Guinea thylacine falls outside the known range of measurements of modern thylacines in at least one character (length of  $P_3$ ). Hobart Van Deusen has a full description of the specimen in preparation for the Novitates series of The American Museum of Natural History. It is hoped that a  $C^{14}$  date will also be available.

*Origins.*—The origin of the Thylacinidae is not yet known although Stirton *et al* (1961, p. 35) have suggested that a dasyurid fossil (comparable in size with *Dasyurus viverrinus*) found in Lake Napakaldi in Central Australia may possibly be ancestral because it possess three premolars, graded from front to rear, and lacks a metaconid on  $M_1$ . But other Dasyuridae (see below) possess a very reduced metaconid on  $M_1$  and others have three premolars graded from front to rear and it seems far more likely that a more significant feature of the thylacinid lower dentition, and the one in which it differs from that of advanced Dasyuridae like *Sarcophilus*, lies in the development in thylacine lower molars of a main posterior shearing crest along the ridge from protoconid to hypoconid; this bypasses the metaconid. In the dasyurid line

Fig. 7.—Cusps of the upper and lower maxillary teeth of Dasyuroidea. Right upper tooth rows and left lower rows illustrated. Note main differences between *Thylacinus* and others are (a) uppers: *Thylacinus* has poorly developed stylar cusps; (b) lowers: *Thylacinus* has main shearing crest to hypoconid from protoconid; *Dasyurus* and *Sarcophilus* have this to metaconid (pa paracone, pr protocone, me metacone, prd protoconid, pad paraconid, med metaconid, end entoconid, hyd hypoconid, hyld hypoconulid). Ridges are shown in continuous line, valleys in broken line.

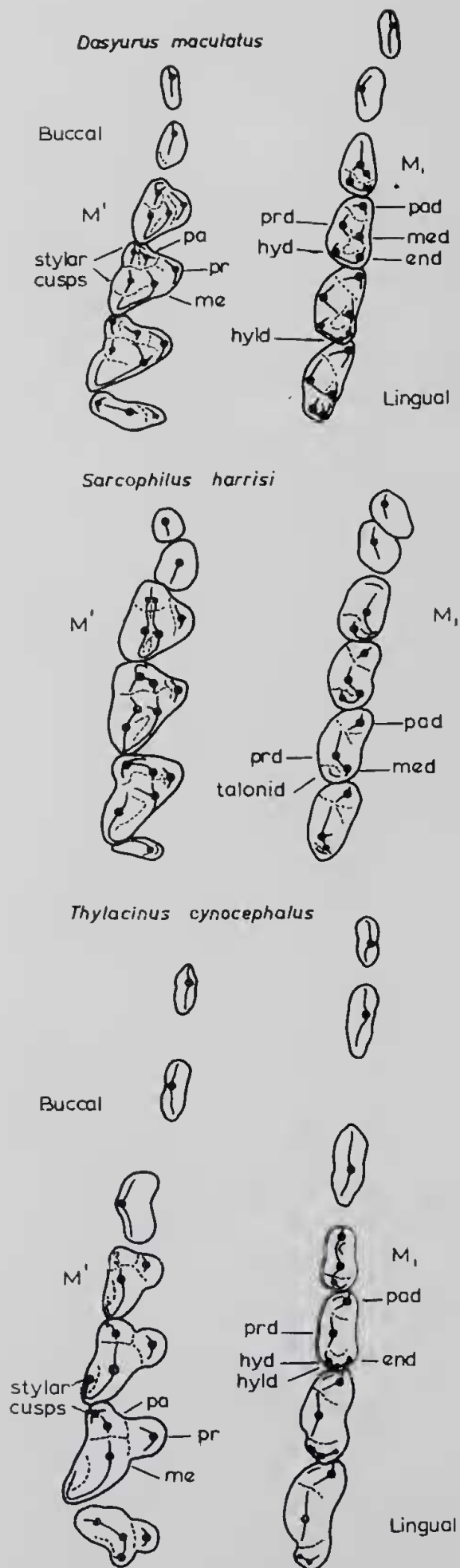


Fig. 7.

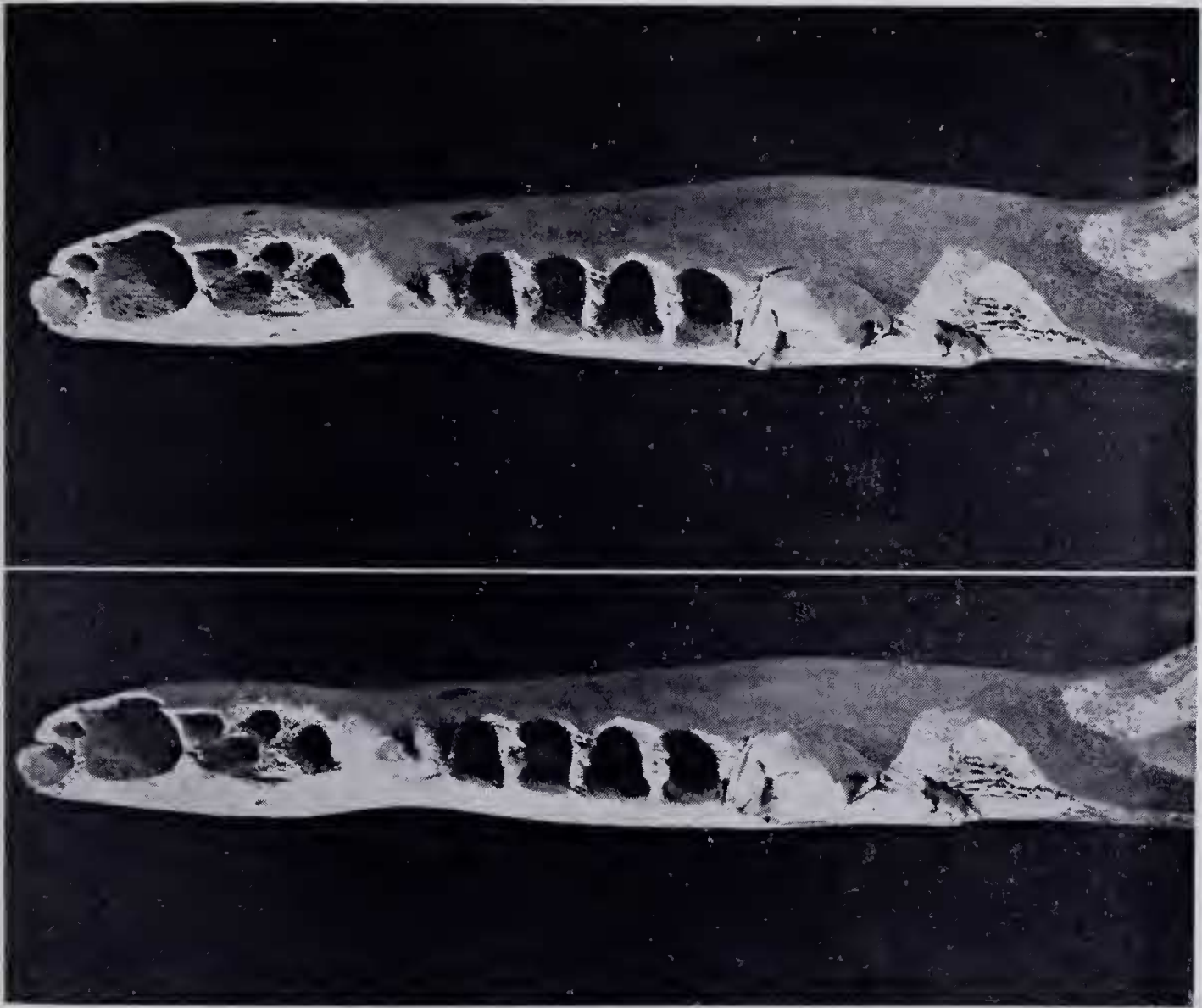


Fig. 8.—Holotype of *Glaucodon ballaratensis* Nat. Mus. Vict. No. P16136 Magnification X2. (Stereo-pair by courtesy Nat. Mus.)

the shearing ridge which is developed is that which runs from the apex of the protoconid; through the tip of the metaconid to the entoconid; in its fully developed form the metaconid is absorbed without trace into this ridge. In both kinds of specialization the metaconid is reduced as its end product, but in the thylacinid line the shear is developed by accentuating the talonid and the hypoconid crest, in the dasyurid line it is developed by specializing the metaconid crest and reducing the talonid (see fig. 7).

Dasyuridae with three premolars which increase in size from front to rear include *Sminthopsis rufigenis*, *S. ferruginifrons*, and *Murexia maxima* (Tate 1947, p. 151, table 5). The metaconid of  $M_1$  is so reduced as almost to be absent in the newly described *Antechinus rosamondae* Ride, 1964a (specimen W.A.M. No. M 3421).

#### Dasyuridae Goldfuss, 1820

##### Dasyurinae

The subfamily Dasyurinae includes a wide range of native cats and their allies including the so-called marsupial mice. It excludes the

Myrmecobiinae (the marsupial Banded-anteater). From morphologically greatest to the least, species range from the massive Tasmanian Devil, *Sarcophilus*, through the more typical *Dasyurus*\*, the arboreal treeshrew-like *Phascogale*, their terrestrial relatives *Dasyercus*, the smaller *Antechinus* and *Sminthopsis*, to the minute *Planigale*.

Few fossil dasyurines are known. The oldest is probably the as yet undescribed form mentioned by Stirton *et al* (1961, p. 35) from the

\* I follow Simpson 1945 in rejecting Pocock's (1926) concept of four generic names for five species of very similar spotted native cats. These additional "genera" *Dasyurops*, *Dasyurinus*, *Satanellus*, are based in the main upon slight variations in the development of the great toe and in the nature of the footpads. If similar reasoning was to be applied to the related genus *Sminthopsis* (which mercifully has so far evaded the attentions of the splitter) we could have in Western Australia alone up to six "genera" of these. Pocock is also well known as a splitter of eutherian cats (see Simpson 1945, pp. 231, 2 for remarks on this and a rather diverting comment on the philosophy of splitting as applied to cats) but it is not generally realized that the present situation in marsupial "cats" is also due to Pocock's attentions.

Etadunna (?Mioc.) formation. This unnamed species has been discussed above under Thylacinae.

The most important fossil dasyurid yet described is *Glaucodon ballaratensis* Stirton, 1957; its age is not known but is possibly Pliocene (see below). Several Pleistocene species of modern genera have been described. These give little information of phylogenetic importance except perhaps of gigantism.

*Glaucodon ballaratensis* Stirton, 1957

*Glaucodon* is known from a single almost complete right mandibular ramus which lacks all teeth but the first and fourth molar (fig. 8). It was found in a well at a depth of fifty feet near Ballarat and reached the National Museum of Victoria in 1914. Gill (1957, p. 191), in describing the site, commented that an intensive study is needed before the fossil can be dated with accuracy but the materials in which the well was sunk appear to have been laid down subsequent to the eruptions of the volcanoes which are represented today by Mount Moorookyle and McRorie's Hill. He considers that the deposit is either Pleistocene or Pliocene.

Irrespective of its as yet undetermined age, the fossil is of great interest because it is morphologically intermediate in its few characters between the "normal" large Dasyuridae (e.g., *Dasyurus maculatus*) and the more specialized short-faced Tasmanian Devil *Sarcophilus*. In the skull, these two sorts of Dasyurinae differ principally in the characters associated with the greatly shortened face of *Sarcophilus* coupled with its more extreme development of "carnassial" dentition of the pseudocreodan type (see Butler 1946); in *Sarcophilus* great emphasis has been placed on the paraconid crest (particularly between paraconid and protoconid) and the talonid and metaconid are reduced as compared with the ancestral didelphid or even dasyurid molar type (fig. 7). Shortening of the face is a trend which is often repeated among Dasyurinae and it commonly finds expression in reduction and crowding of premolars; examples of it are *Antechinus rosamondae* which may be compared with *A. flavipes*, and *Dasyercus cristicauda* which may be compared with *Phascogale*. Even *Dasyurus* has lost one of the original number of three premolars so that, even in this long-faced genus, shortening has occurred to some extent.

The molar teeth of *Glaucodon* are shown in stereoscopic pair in fig. 8.

In  $M_1$ , the protoconid is large, there is no paraconid, the metaconid is a small but distinct cone adpressed to the protoconid. The talonid is about one-third of the total length of the tooth. The hypoconid is well developed, the entoconid is small, and there is possibly a small hypoconulid between them. Since the metaconid of  $M_1$  is barely present in *Sarcophilus* and it is often almost completely reduced in *D. maculatus*, this tooth may be somewhat more primitive in this respect than either; however the metaconid is closely adpressed to the protoconid and the tooth is particularly reminiscent of that of *Sarcophilus* in its massiveness and lack of lateral compression.

In  $M_1$ , the protoconid is large and tall and the paraconid is also well developed. The metaconid is somewhat smaller. The main shearing crest of the tooth comprises the ridges from the apices of the paraconid and protoconid, and that between the protoconid and the metaconid (which is set lower than the paraconid). The talonid is much reduced and consists of little more than a hypoconid. The disparity between the heights of the paraconid and metaconid (compare 3 and 4 of Table 3) is a *Sarcophilus*-like character not seen in *D. maculatus* where these two lingual cusps are more or less equal. Although, as mentioned below, the talonid of the  $M_1$  of *D. maculatus* may be reduced as much as in *Glaucodon*, in *D. maculatus* the hypoconid and entoconid are separate and even a hypoconulid may be present. In *Sarcophilus* the talonid is usually represented by little more than an isolated cuspule (possibly the hypoconid) posterobuccal to the metaconid, a condition morphologically more like that of *Glaucodon* although advanced on it.

There are few characters in *Glaucodon* upon which to base detailed comparison. However, these are compared with *Sarcophilus* and *Dasyurus maculatus* in Table 3 (and in figs. 7 and 8). In these few characters the more highly specialized *Sarcophilus* differs from the less specialized *D. maculatus* in having:

- (a) An enlarged molar trigonid in comparison with its talonid; in particular it has almost totally reduced the talonid in  $M_1$  (2 of Table 3). The trigonid of  $M_1$  is also compressed bucco-lingually.
- (b) A paraconid which is increased in height relative to the protoconid (3 of Table 3).

TABLE 3.

Comparison of characters of *Dasyurus maculatus*, *Glaucodon* and *Sarcophilus*.

	<i>D. maculatus</i>		<i>Glaucodon</i>	<i>Sarcophilus</i>	
	n.	range %	%	range %	n.
1. Total length of $M_{1-1}$ as % of length of mandible from anterior tip of posterior edge of masseteric shelf ..	3	29.8-33.2	39.6	37.8-42.7	7
2. Length of $M_1$ excluding talonid as % of total length of $M_1$ ..	5	67.7-77.1	77.0	92.0-97.4	8
3. $M_1$ height of paraconid as % of protoconid ..	5	52.6-63.3	56.1	63.4-72.2	6
4. $M_1$ height of metaconid as % of protoconid ..	5	52.6-60.7	42.7	31.3-38.0	6
5. Depth of mandible expressed as % of length of mandible from anterior tip to posterior edge of masseteric shelf ..	4	15.7-16.7	20.5	21.7-23.0	7
6. Depth of mandible expressed as % of molar tooth row ..	3	49.8-56.2	51.9	51.5-58.9	7

- (c) A metaconid which is reduced in height. This is almost a vestige in some molars (4 of Table 3).
- (d) Incisor alveoli which are much crowded so that the alveolus of the second incisor is raised above the plane of the other two (this condition occurs in *D. maculatus* but it is not as well marked).
- (e) Premolar alveoli which are crowded, each pair being set at an angle to the long axis of the ramus. There are no diastemata between them.
- (f) The depth of the mandible is proportionally greater in comparison with its length (5 of Table 3).
- (g) The molar tooth row is proportionally longer in comparison with the length of the mandible (1 of Table 3).

*Glaucodon* compares with these in the following way:

- (a) The trigonid of  $M_1$  is compressed buccolingually and the talonid is more reduced than in most *D. maculatus* (although I have measured a specimen of *D. maculatus* which had a talonid which was reduced to a similar degree—see Table 3).
- (b) The height of the paraconid of  $M_1$  as compared with that of the protoconid is within the range of *D. maculatus* and not of *Sarcophilus*.
- (c) The metaconid is greatly reduced towards the condition in *Sarcophilus*.
- (d) The incisor alveoli are as in *Sarcophilus*.
- (e) The premolar alveoli are as in *Sarcophilus*.
- (f) The depth of the mandible, expressed as a percentage of its length, is intermediate between that of *D. maculatus* and *Sarcophilus*.
- (g) The length of the molar tooth row, as a percentage of the length of the mandible, is within the range of *Sarcophilus* and not of *D. maculatus*.

In all, as far as its known characters go, there is little doubt that *Glaucodon* can be regarded as structurally ancestral to *Sarcophilus*. In some characters it still lingers on the *Dasyurus* side and in others it is clearly *Sarcophilus*-like. In one character (the well developed conical but adpressed metaconid on  $M_1$ ) it is like neither.

#### *Dasyurus affinis* and *D. bowlingi*

*D. affinis* McCoy (?1862) and *D. bowlingi* Spencer & Kershaw (1910) are the only two species of fossil *Dasyurus* which have been described to date.

The name *D. affinis* was published in Quarter Sheet N.W. of the Geological Survey of Victoria in a note which merely states "*Dasyurus affinis* (McCoy) New Species nearly as large as *D. maculatus* but differing in proportions". The material comprises two syntypical left mandibular rami (Nat. Mus. Vict. P 7426, P 15101) which have since been figured by Gill (1953b). Gill advises me that the precise locality of the cave from which the specimens come is in basaltic

tuff, under a flow of Newer Basalt on a small tributary near the head of Toolern Creek, 4½ miles S. of Gisborne and 1½ miles S.W. of Couan-galt Post Office. The material is Holocene and no revision of the status of the species has been published to date.

*D. bowlingi* is from the dune sands of King Island and Deal Island in Bass Strait and the measurements and other data presented by Spencer & Kershaw of a good series of specimens suggest that the species was much larger and also morphologically distinct from *D. maculatus* with which it was sympatric. The geological age of the material is not known but Spencer & Kershaw infer that the species persisted into modern times and was seen alive by Péron during the Baudin expedition of 1801.

#### *Scarcophilus lanarius* and *S. prior*

*S. lanarius* (Owen, 1838) and *S. prior* De Vis (1883) are the only two species of fossil *Sarcophilus* which have been described to date although Stirton (1957, p. 131) records an undescribed species from the Pliocene at Kalamurina, on the Warburton River, South Australia, which he says is closer to *S. lanarius* than to *S. harrisi* Boitard (the modern species).

It is widely accepted that *S. lanarius* is a gigantic Pleistocene form of the modern species and Gill's (1953, p. 87) statement of mandibular measurements "from 15 to 50 per cent. larger than the average extant *Sarcophilus*" suggests that, unlike the position in *Thylacinus spelaeus* and *cynocephalus*, the distinction between the two should be maintained.

*Sarcophilus prior* De Vis, 1883 comprises only the proximal articular surface of a right tibia with a little of the shaft. It is from "Darling Downs" and is somewhat larger than the corresponding bone in the modern specimen of *Sarcophilus* with which De Vis compared it.

#### Myrmecobiinae

There are no fossils and nothing significant has been added to the problems of the affinities of *Myrmecobius* since the beginning of the century. During the 19th century *Myrmecobius* was believed to be an unmodified survivor from the Jurassic with affinities with Mesozoic mammals, but the modern view which can be directly attributed to Bensley is that its unusual dental characters (and among these its high dental formula) have been derived from those of normal Dasyuridae. Bensley (p. 100) said that many of the characters of the incisors, canines, and premolars "which appear at first sight to be primitive, are repeated in the Peramelidae, where they are undoubtedly the result of retrogression. The patterns of the lower molars are directly derivable from those of the smaller Dasyurinae", and of the upper molars Bensley is also of the opinion that the basic pattern which can be recognized running through these very variable teeth is approximately that characteristic of normal Dasyurinae as well. Great dental aberration is characteristic of myrmecophagous mammals (e.g. *Proteles*, the Aard-wolf).

For a while, the phylogenetic picture was somewhat confused by the description of the fossil *Myrmecoboides* (Gidley, 1915) from the

Mid Palaeocene of North America. This now turns out to be a eutherian insectivore and may be disregarded in this context (Simpson 1945, p. 172).

### PERAMELINA

Even less is known of the Peramelina as fossils than the Australian Marsupicarnivora with the exception of enormous numbers of specimens of modern species in the Pleistocene cave deposits of various parts of Australia.

The modern bandicoots appear to fall into at least two distinct groups, one of these includes only the Rabbit Bandicoots (*Macrotis*) while the others are obviously fairly closely related, with the Pig-footed Bandicoot (*Chaeropus*) as a highly specialized derivative. *Perameles tenuirostris* Owen, 1877 and *Perameles wombeyensis* Broom, 1896b have both been described from the Pleistocene of New South Wales.

There has been no revision of the status of *P. wombeyensis* but, from what I know of the fauna from the Wombeyan Caves, N.S.W. which contains it (Ride 1960) I would not be surprised to find that it is identical with a modern form.

*Perameles tenuirostris* (Owen 1877, Pl. V., figs. 10, 11) is from the Wellington Caves, N.S.W. and is stated by Lydekker (1887, p. 255) to be identical with the modern *P. nasuta*.

*Ischnodon australis* Stirton (1955) is the only Tertiary species which has been described.

#### *Ischnodon australis* Stirton, 1955

This fossil bandicoot which comprises a single fragmentary mandibular ramus with two pre-molars and two molars in position was described from the late Tertiary Palankarina Fauna from the Mampuwordu Sands at the Woodard Quarry near Etadunna Station, South Australia. Stirton was unable to determine the exact relationship of the bandicoot (see Fig. 9) but he suggested that it was nearer to the rabbit bandicoots (*Macrotis*) than to other Peramelidae. In particular, he considered that the presence of a somewhat reduced paraconid and reduced hypoconulid on the molars indicated relationship to *Isoodon* and *Perameles* but the fact that they were reduced although present suggested *Macrotis* relationships where (he implies) the paraconid is lost.

Comparison of Stirton's figure and measurements with *Macrotis* in the collection of the Western Australian Museum reveal that his generic diagnosis includes some specimens of *Macrotis lagotis* because some of the details of dentition which he regarded as being of generic value, i.e. the presence of a much reduced paraconid and hypoconulid, and the presence of a small styler cusp antero-buccal to the hypoconid, are very variable in that species. In fact all these characters of *Ischnodon* are present in specimens WAM No. M 1399 from Bridgetown in south-western Australia, and WAM No. M 632

from Laverton, W.A., yet, as Stirton has implied, other specimens lack the paraconid completely (e.g. WAM M 898 from Wiluna).

The only feature of *Ischnodon* at present described which I consider to be of significance are its low crowned molars which are lower than those of any rabbit bandicoot known to me. For the present, the generic distinction can only be maintained in this respect.

### DIPROTODONTA

The Diprotodonta is the most diverse, and to me most structurally interesting, of all the marsupial orders. It is generally thought of as a herbivorous order but it actually contains a complex series of radiations within itself. Primitive modern members of it (Bensley 1903, p. 124) are insectivores (e.g. the small modern phalangiers such as *Distoechurus* and *Cercartetus*, and in addition it contains at least one rapacious carnivore (*Thylacoleo*), and several smaller modern forms with strong carnivorous tendencies (*Bettongia*). There are many herbivores of browsing and grazing habit and there is even a fossorial bear-like animal (the Wombat). Among the browsers and the grazers were the heavy "pachydermatous" Diprotodontidae, the gazelle and cervid-like Macropodinae, and their close relatives the browsing-adapted bovid-like Sthenurinae (see Ride 1959 discussion of *Procoptodon*). Some of these phyla have even become convergent upon each other as have the diprotodontid palorchestines upon kangaroos (Woods 1958, Bartholomai 1962).

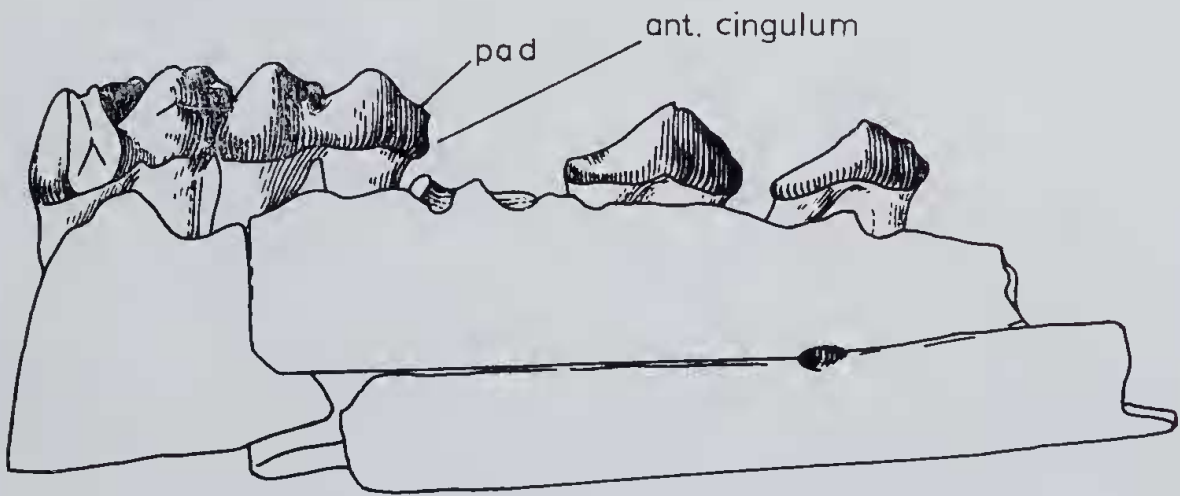
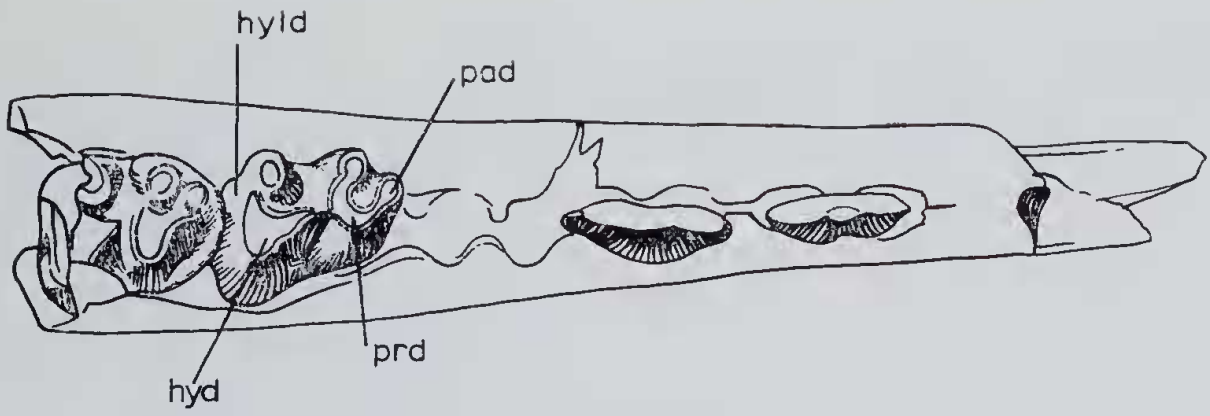
The known Pleistocene fossils, of which there are many, are mainly of large and moderately large animals and help us to fill out the details of this great radiation; the great numbers of them and their diversity gives to Diprotodonta a much better appearance of balance of knowledge between fossils and living genera. However these appearances are still misleading because we have no lineages and thus can talk only of evolutionary lines by arranging Recent or Pleistocene animals in order of primitiveness and arguing from them.

The sub-taxa of Diprotodonta which may be distinguished by this means comprise five and possibly six distinct phyletic lines. These are the Phalangeridae as represented by the modern Australian Possums, Cuscuses, Flying Possums, Pigmy Possums, etc. and Pleistocene forms including *Thylacoleo*; the Macropodidae as represented by the modern Kangaroos, Wallabies and Rat Kangaroos (these latter may be widely separate from true Macropodidae and, in modern taxonomic practice it is usual to separate them off as a subfamily Potoroinae); the Diprotodontidae as represented by the giant extinct forms *Nototherium*, *Diprotodon*, *Palorchestes*, etc.; the Vombatidae which comprises the Wombats and their extinct giant relatives; and the Wynyardiidae which contains only *Wynyardia bassiana* of

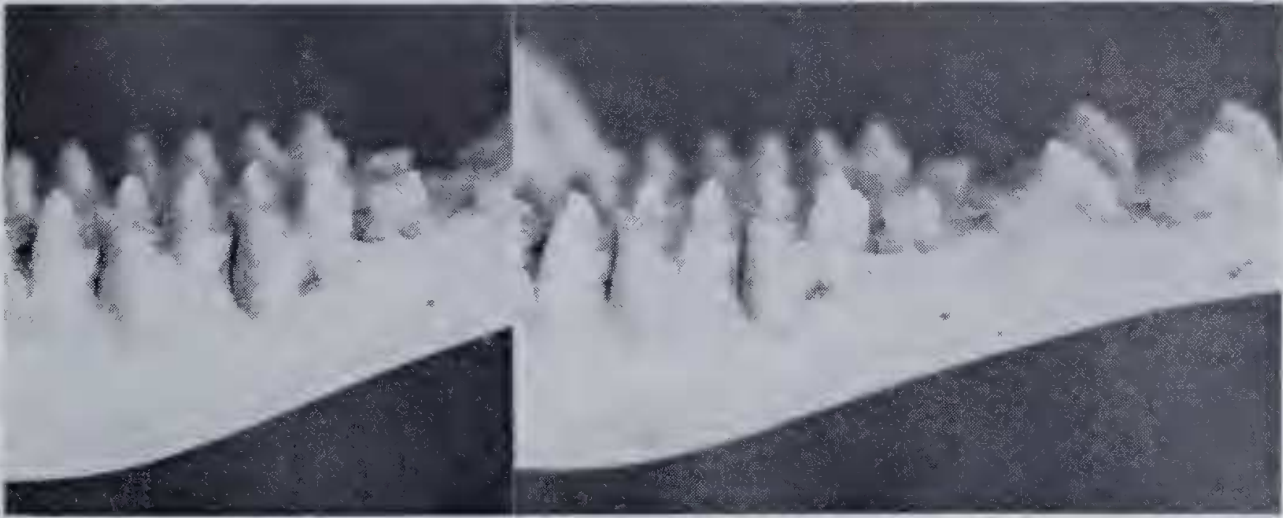
Fig. 9 (opposite).

Fig. 9.—Upper figure: Holotype of *Ischnodon australis* after Stirton 1955. Stereo-pairs of mandibles of *Macrotis lagotis* for comparison of paraconid, hypoconulid and cuspule between protoconid and hypoconid. (Upper pair WAM No. M632, Laverton, W.A. Lower pair WAM No. M1399, Bridgetown, W.A.) Upper pair show dP<sub>4</sub> in position. In lower pair P<sub>4</sub> is erupting. Stereo-pairs and line drawing not to same scale.





1 cm



the Oligocene. In addition there is possibly a separate line containing only the Koala *Phascolarctos* (see Troughton 1959, pp. 75 and 84 for a discussion of the problems of the relationships of *Phascolarctos*).

Wynyardiidae Osgood, 1921

*Wynyardia bassiana*

The oldest diprotodont known to us is *Wynyardia bassiana*, a remarkably complete and semi-articulated skeleton from the Oligocene which was found prior to 1876 at Fossil Bluff near Wynyard in Northern Tasmania. It received numerous mentions in literature (Gill 1957) before being described by Sir Baldwin Spencer in 1900 (Spencer 1901). Unfortunately, Spencer was so impressed by its great age (at that time thought to be basal Eocene) that he made rather extravagant claims for it on the basis of a detailed description and discussion of its characters—a discussion based upon inadequate\* material of other marsupials.

Spencer concluded that *Wynyardia* was intermediate between the "Pelyprotodonts" (Marsupicarnivora and Peramelina) and Diprotodonts and moreover that it possessed a number of characters unknown in any other marsupial. Subsequently, Wood Jones became interested in this fossil and ultimately obtained the loan of its principal parts for redescription. Unlike Spencer, he concluded that the fossil had no non-marsupial characters, that it had no specifically non-diprotodont characters, and that it must be considered an ally of the phalangers but probably differed from the modern lightly built animals in both gait and bodily habit.

Unfortunately, Wood Jones, always a direct man, demonstrated his disagreement with Baldwin Spencer's conclusions in a manner which has allowed subsequent workers to misinterpret his results and moreover to misread his conclusions. Thus *Wynyardia* has come to be regarded as an animal very much like the modern possum *Trichosurus* (see Gill 1957). Admittedly, Wood Jones claimed that *Wynyardia* had many resemblances to *Trichosurus* but this claim was in the main because his results were based almost entirely upon comparison between the fossil and a similarly mutilated specimen of *Trichosurus* (see Wood Jones 1931).

Thus a suspicion arose that *Wynyardia* might even have been a modern possum which had fallen into a fissure in the limestone and had become incorporated into the Fossil Bluff sequence (Gill 1957 gives an excellent account of this).

The most important recent work on *Wynyardia* has been done by E. D. Gill, Curator of Fossils at the National Museum of Victoria. By using physical and stratigraphical methods he re-examined the provenance of the fossil and concluded that it was undoubtedly contemporary

\* Comparison by Spencer with an inadequate series and insufficient information regarding variation is the only way in which I can interpret the mis-statements of marsupial anatomical detail which he makes. The mis-statements do not relate so much to the fossil (of which his description is excellent) but in regard to the distribution of various characters among living Marsupialia.

with the Fossil Bluff fauna and is not a subsequent inclusion. Today, this fauna is considered to be Oligocene‡ (Gill 1962, p. 249).

The establishment that the fossil was genuine together with the misinterpretation of Wood Jones' results has resulted in claims being made that the Possum (i.e. *Trichosurus*) has an antiquity dating back to the Oligocene (see Gill, 1955, p 92). Results of examination by myself (the full details of which will be published elsewhere) do not support this view and reveal that, contrary to current opinion (which has grown like a snowball around a slender nucleus of misinterpreted results), *Wynyardia* is a very remarkable animal quite unlike any known diprotodont combining as it does a number of very primitive marsupial characters with robustly expressed specializations peculiar to itself. Any resemblance to *Trichosurus* which the fossil possesses is in those characters which represent relatively unspecialized diprotodonty.

*Wynyardia* comprises a broken skull (fig. 10), the inferior border of the left mandibular ramus, a coronoid process (which has become lost since Spencer's examination), the axis vertebra, a series of nine articulated presacral vertebrae including the last thoracic, portions of fused sacral vertebrae, a large portion of pelvis comprising the dorsal ramus of the right ischium including the acetabulum, and a more or less complete right ileum, one epipubic bone, a more or less complete left femur and a fragmentary right femur, the left tibia and fibula, together with some fragments of ribs. At the time of Baldwin Spencer's and Wood Jones' examinations, the skull, mandibular ramus, long bones of the hind limb, sacrum, and pelvic fragments had been extracted from the matrix. After Wood Jones examined the material, the vertebral column had also been extracted and was available for examination. The otic region was still filled with matrix and glue and I removed these.

That *Wynyardia* is a diprotodont is established by the presence, at the anterior end of the mandible, of the unmistakable root of a single large incisor and as Wood Jones pointed out, the upper incisor alveolus which remains in the premaxilla is consistent with its having an enlarged first upper incisor of phalangerid type. Along the broken dorsal margin of the mandibular ramus there are four circular structures which are almost certainly the broken tips of the roots of cheek teeth, these are followed by a pathological cavity and what is almost certainly the alveolus of the last molar. If this mandible and these "teeth" are then positioned on the skull it will be seen that the anterior end of the zygomatic arch lies midway along the toothrow; this is another diprotodont character not found in Dasyuridae or Peramelidae. In these it lies at the posterior end of the toothrow. The position of the posterior end of the palate is indicated by the pterygoids and confirms this. The pterygoid fossa in the mandible can also only be matched in Diprotodonta among Australian forms.

‡ Spencer's geological contemporaries regarded it as "basal Eocene" while Wood Jones followed Chapman's "no older than the Miocene" and Howchin's "no older than the Pliocene" (Jones 1931, p. 97).

Primitive characters found in no diprotodont are best seen in the region of the middle ear (see stereo pairs in fig. 10 a, b). Unfortunately, the bullar wing of the alisphenoid has been broken away and the tympanic is missing but sufficient completely undamaged surface on the post-glenoid process remains to show that the tympanic was not tubular and fused to the post-glenoid process as in Diprotodonta. In spite of Wood Jones' statement that the post-glenoid process and the auditory region do not differ from that of *Trichosurus*. He argued that the smooth surface of the post-glenoid process might be due to erosion but this is not so; except for about 3 mm of its postero-mesial end (length 12 mm), the structure is covered by a finished surface which is quite unlike the ragged cancellar appearance of an eroded contact area from which a fused tympanic tube has been torn. On the other hand, I suspect that the innermost 3 mm which is eroded does represent the point of contact with the tympanic ring (the differences between the post-glenoid and tympanic region of *Wynyardia* and *Trichosurus* can be seen in fig. 10 b, d) and if this is so, it could represent an intermediate stage between the free ring of Didelphidae and the fused tube of the Phalangeridae.

The most important primitive character of the middle ear of *Wynyardia* is the complete absence of epitympanic sinuses either anterior or posterior to the epitympanic recess. Van der Klaauw (1931, p. 82) says that these sinuses are absent in monotremes and didelphids, while other marsupials show well-developed sinuses in the squamosal. The very small epitympanic recess between the periotic and the portion which remains of the tympanic wing of the alisphenoid suggests that the alisphenoid bulla was at most very short and merely shielded the epitympanic recess. In fact, in general appearance the whole region is almost identical with that of modern *Didelphis virginiana* (fig 10 c) except that the anterior face of the periotic is slightly more flattened in the fossil which suggests that the tympanic wing might have contacted it here. The morphology of the squamosal behind the ear and its entire relations in the nuchal and post-glenoid regions are also completely unphalangerid and can be matched only in Marsupicarnivora.

Other characters of a marsupicarnivoran aspect, although probably of less importance being inherited by other Diprotodonta, are the shape of the nasals which are precisely those of *Didelphis*, the lachrymo-nasal contact, the great sagittal crest, the very short post-tympanic region, and the position of the sacral articulation in the ilium. This is very far anterior as in *Didelphis*, not mid-way to the acetabulum as in Phalangeridae. The triangular cross section of the ilium is also typically *Didelphis*-like.

Some of the specializations of *Wynyardia* seem to be related to its extremely robust build and, probably, erect carriage of the body which must have been somewhat Koala-like. This robustness is represented in the skull by the depth of the mandible (only the tips of the roots of the cheek teeth are present along the broken dorsal surface so that it seems certain that much

is missing of the ramus which is already not much more slender than the mandible of *Trichosurus*) and by the large areas of attachment of the pterygoid and masseter-temporal muscle groups. It is in the post-cranial skeleton however that adaptations to an erect or semi-erect posture are most marked. Lumbar vertebrae, which are typically phalangerid in possessing well developed slender anapophyses (hyposphenes), have transverse processes which are horizontal and form an acute angle with the plane of the anterior zygapophyses. This acute angle is only exceeded by the Koala (and approached by the cuscus). The koala and the cuscus are both animals which habitually adopt an erect position. The pelvic girdle suggests the same conclusion. The epipubes are very large; in modern Diprotodonta they are largest in the Koala (approximately half the length of the femur); in *Wynyardia* even the incomplete epipubis is greater than half the length of the femur (64.7 mm: 106.4 mm). On the ilium, which is triangular in section, the area of origin of the gluteus medius is large (see Elftman 1929 for terminology) which agrees with the observation that the greater trochanter of the femur (which carries its insertion) is also large. On the other hand the lesser trochanter is smaller than that of *Trichosurus* or *Phalanger* and this agrees well with the observation that the area of origin of the iliacus on the ilium is smaller in *Wynyardia* than in these genera. The acetabulum is strongly buttressed anteriorly. These features would argue (see Elftman 1929, p. 213) that the animal was able to remain for considerable periods in the upright position where the gluteus medius would be one of the muscles concerned in its support.

The bones of the hindlimb are robust and the tibia is short as compared with the femur. The fibula is also much closer to the tibia in size than is that of modern phalangerids (e.g. *Trichosurus*). However, it is of phalangerid form as distinct from that of Macro podidae or Peramelidae (see Barnett & Napier 1953, p. 209). In all, it would seem that the specializations of the postcranial skeleton and in particular the robustness of the bones of the hindlimb, the proportions of tibia and fibula, and the shortness of the distal part of the limb in comparison with the femur, suggest that *Wynyardia* was a slow, deliberately moving animal without saltatory or cursorial specializations.

Since *Wynyardia* is so very different from all known phalangerids—an Oligocene diprotodont with clear evidence of marsupicarnivoran origins of a didelphid kind, but yet highly specialized in its own peculiar way—I follow Osgood (1921) in including it in a separate family which will include those primitive diprotodonts which combine diprotodonty with a primitive middle ear which (like that of *Didelphis*) lacks epitympanic sinuses.

#### Phalangeridae Thomas, 1888

The Phalangeridae is the stem family of the Diprotodonta with the Wynyardiidae (as defined here) at its base; although the *Wynyardia* itself is probably too specialized to be directly

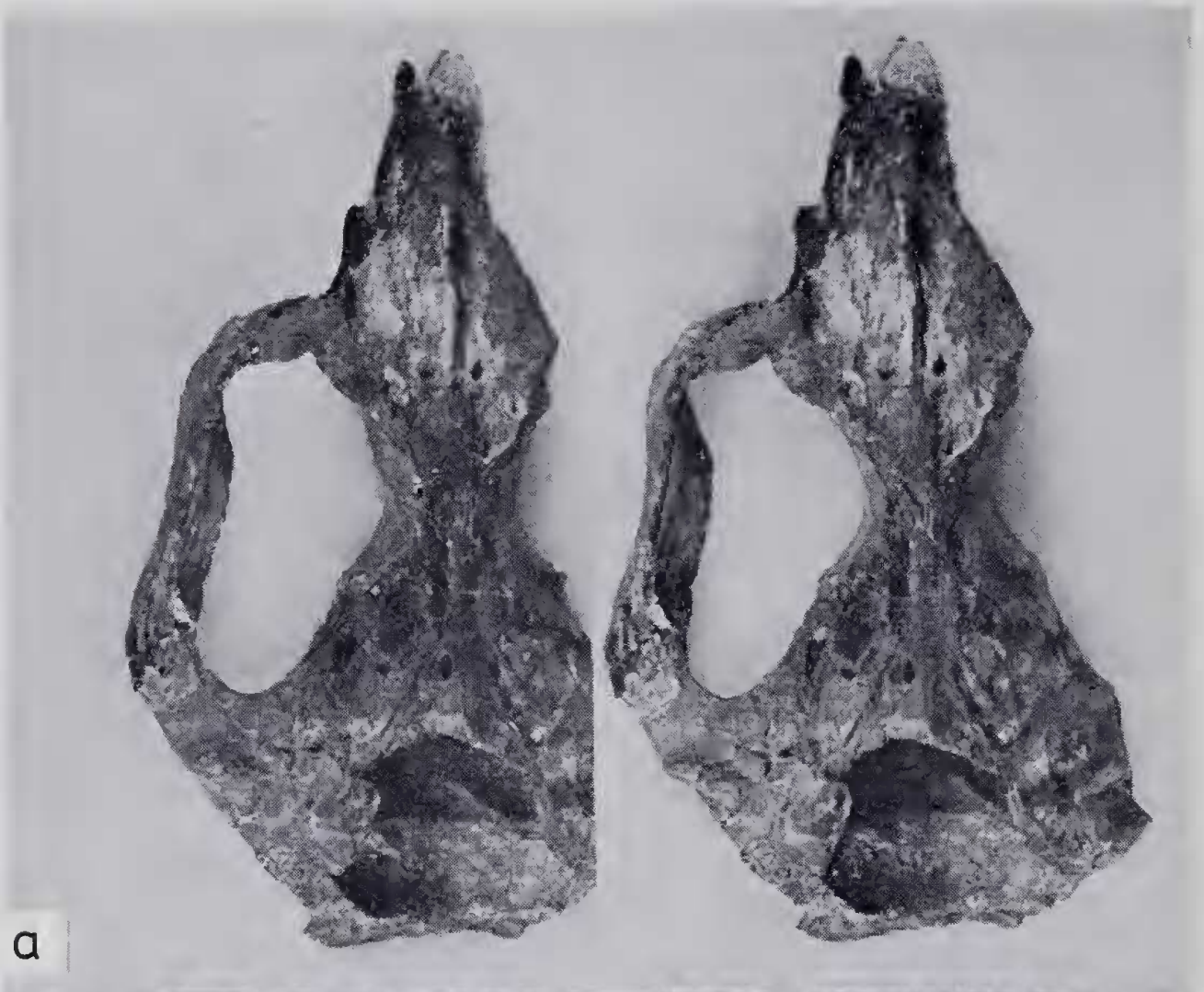
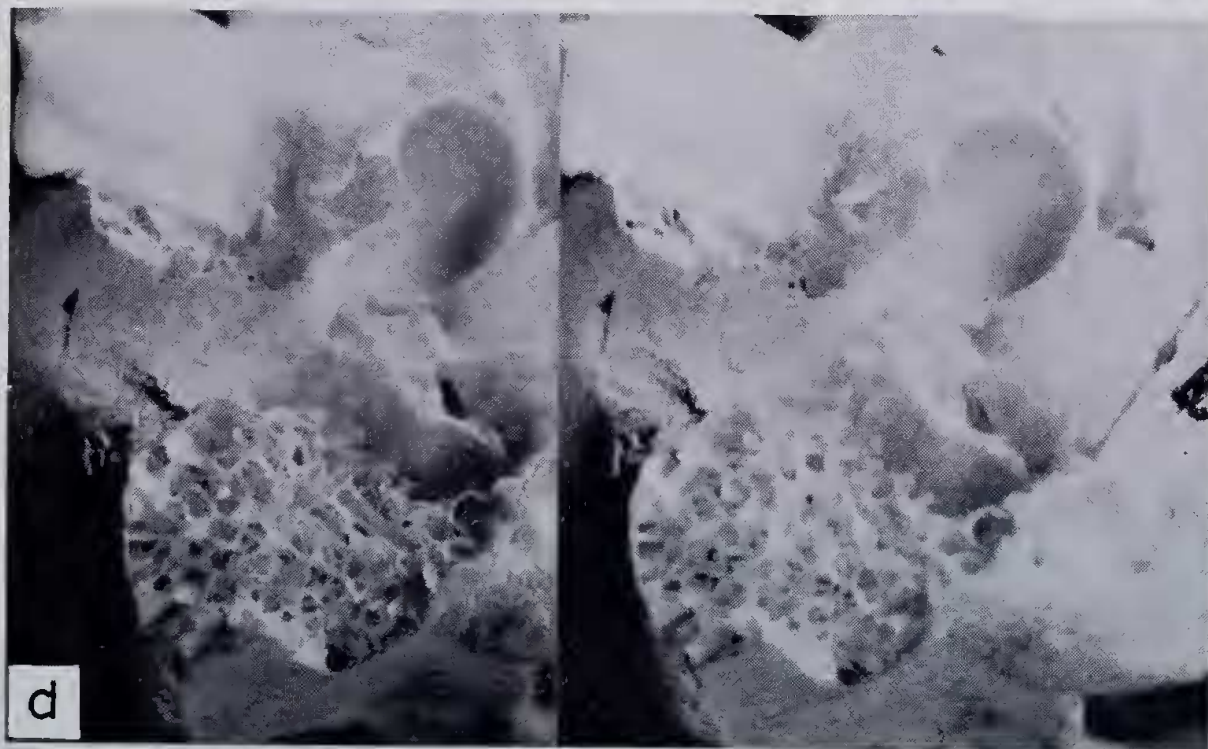


Fig. 10.—*Wynyardia bassiana*. (a) Ventral view of skull. (b) Otic region. (c) Otic region of *Didelphis virginiana* for comparison. (d) Otic region of *Trichosurus vulpecula* for comparison. In *Trichosurus* the tubular tympanic meatus has been broken away from the post-glenoid process and from the squamosal. The floor of the alisphenoid bulla has also been removed to reveal the epitympanic sinuses for comparison.



ancestral. Offshoots which are probably pre-Miocene in time of separation are the Vombatidae, the Diprotodontidae, and the Macropodidae.

The main stock is the Phalangerinae, a subfamily which contains all of those forms which Bensley regards as basal in dentition to the phalangerid radiation (including *Acrobates*, *Distocheurus*, *Eudromicia*, *Cercartetus*), as well as certain larger forms which have progressed beyond the insectivorous habit but which, nevertheless, have remained rather generalized in molar form (i.e. *Petaurus*, *Trichosurus*, *Wyulda* and *Phalanger*).

The Tarsipedinae, which is probably a relatively modern offshoot, contains only the highly specialized nectar-feeding *Tarsipes* which thus occupies a position analogous with that of *Myrmecobius* in the Dasyuridae; and, as is the case there, fossils are unknown.

The Phascolarctinae, as it is at present recognized, includes the Koala *Phascolarctos*, the ringtails *Pseudocheirus* and the Greater Glider *Schoinobates*. These are selenodont in dentition but there is very great suspicion that too much phylogenetic emphasis has been placed on this character (see below and Troughton 1959, p. 84).

The Thylacoleoninae comprises the marsupial lions. Obviously derived from large phalangers, they represent the supreme diprotodont adaptation to the rapacious habit, a habit which is not strange to some of their smaller relatives. Two species are known. *T. carnifex* Owen is the typical Pleistocene form and *T. crassidentata* Bartholomai (1962) is a slightly less highly evolved form from the Pliocene Chinchilla Sand. Woods (1956) has revised *Thylacoleo*. Gill (1954) discusses habits and distribution and provides a full bibliography.

Most of these forms of Phalangeridae are fairly small animals and accordingly it is not surprising that there are only a few fossils beyond the owl pellet deposits of the Upper Pleistocene and Recent. Of the phalangerid fossils the earliest and most important is *Perikoala palankarinnica* Stirton, 1957a from the Miocene of the Etadunna Formation; a form which Stirton places in the Phascolarctinae.

Of the Pleistocene species of Phalangeridae only one has been sufficiently spectacular to have played an important part in phylogenetic speculation. This is *Burramys parvus* from the Wombeyan Caves of New South Wales. A brief discussion of *Perikoala* and *Burramys* is included here.

#### *Perikoala palankarinnica* Stirton, 1957

*Perikoala* was originally described as part of the Palankarinnina ?Pliocene fauna but Stirton *et al* (1961, p. 36) now refer it to the underlying Miocene Etadunna Formation.

Unfortunately, this remarkable fossil is only known from very fragmentary material: an edentulous maxillary fragment and a broken mandibular ramus with a broken last lower premolar and the first two molars which are almost complete. I have not seen the material but Stirton (1957a) says that it resembles both

*Trichosurus vulpecula* and *Phascolarctos* and he concluded that *Perikoala* was clearly phascolarctine, presumably because of the crenulated enamel in the basins of the teeth and because of the wide separation of hypoconid and entoconid in the posterior premolar which (although only a fragment of it remains) was obviously unusually molarized for a phalangerid. In large Phalangerinae (e.g. *Trichosurus*, *Phalanger*, and *Wyulda*) this tooth is specialized as a sectorial and not broadened as in *Phascolarctos*. As compared with *Pseudocheirus*, *Schoinobates* and *Phascolarctos*, *Perikoala* is not selenodont (or subselenodont) but quadriscuspid or even bilophodont yet it has the large number of small folds in the crenulated enamel so typical of the Koala.

The modern practice of separating the Koala, the Ringtails, and the Greater Glider from the Phalangerinae because of their selenodontology (subselenodontology) follows such authorities on dental morphology as Bensley (1903, p. 135); he and various earlier workers were so impressed by the appearance in some marsupials of selenodont dentition, that they could not avoid drawing parallels between them and the selenodont and bunodont sections of the eutherian ungulates and hence placed great phylogenetic weight on this character. Accordingly, *Phascolarctos* was placed with *Pseudocheirus* and *Schoinobates* in a separate subfamily. The molars of *Perikoala* and *Phascolarctos* are undoubtedly similar in their crenulations but it is timely to remember Thomas' statement (1888, p. 167) in relation to *Pseudocheirus* that "this genus, with its close ally *Petauroides* | *Schoinobates* |, by the complicated subselenodont character of its molars, stands somewhat apart from most of the other Phalangers, and approaches *Phascolarctos*, in which a rather simpler form of the same modification is observable. In young *Cuscuses*, however, a tendency towards the same structure is also visible, but the crests on the molars soon wear off, and then there appears but little difference between their molars and the simple smoothly quadricuspid ones of *Petaurus*, *Dactylopsila*, and their allies."

In fact, one cannot help wondering whether the relationships of *Phascolarctos* and *Perikoala* might not lie with *Phalanger*, rather than with *Pseudocheirus* with which *Phascolarctos* bears scarcely any resemblance except in the questionable selenodontology of its molars. When more is known of *Perikoala*, it may provide a useful indication here.

#### *Burramys parvus* Broom, 1896

*Burramys parvus* Broom is a very small phalangerine with very large sectorial premolars (fig. 11) which closely resemble those of *Hypsi-prymnodon*, (which is in some respects the most primitive of the Macropodidae, and of *Propleopus* the giant Pleistocene rat-kangaroo. Until recently, *Burramys* was only known from a single deposit, the ?Upper Pleistocene Broom fauna of the Wombeyan Caves, New South Wales (Ride 1960). Wakefield (1960) has since obtained it from Buchan in Victoria.

Because of its remarkable premolar, Broom described *Burramys* as a link between the phalangers and kangaroos, and later (Broom 1898) even concluded that it was "probably very closely allied to the small *Phalanger* from which *Thylacoleo* was descended". Ultimately Tate (1948), without further examination, removed *Burramys* into the Macropodidae from the Phalangeridae.

In 1956 I revised the status of *Burramys* following re-examination of some of Broom's original material and some additional specimens which were prepared from breccia collected by Broom at the type locality. *Burramys* was shown to be a phalangerid whose supposed macropod affinities rested solely upon the structure of the premolar, while other characters all argued against such relationships. In particular, these are the structure of the third premolars, the nature of replacement of the milk

premolar (the peculiar "double" replacement of Macropodidae is absent and specialization of  $P_3$  has proceeded in the opposite direction) and the structure of the masseteric fossa together with the absence of a masseteric canal. The case for special thylacoleonine affinities is equally slender and rests upon no more than the enlarged sectorial, a character which is likely to be convergent since the teeth of the "plagiaulacoid" type have been developed independently by at least phalangers, macropods, caenolestoids, multituberculates, and tarsioids (Simpson 1933).

It is very probable that *Burramys* is a member of an aberrant line of Phalangerinae possessing some relatively unspecialized characters, e.g., a *Distoechurus*-like palate and quadricuspid bunodont molars, but also some very specialized ones such as large grooved sectorials, reduced fourth molars, and elongate incisors, characters which probably point to some peculiar insectivorous (or microcarnivorous) adaptation.

#### Macropodidae Gray, 1821

As many fossil species of the family of kangaroos and wallabies have been described as all other Australian fossil marsupials put together. To anyone who knows our present marsupial fauna this is scarcely surprising because, quite apart from their commonness, macropods are generally fairly large animals, are often gregarious and are the dominant herbivores (as they probably were during the Pleistocene as well); it is thus likely that they provided the main source of prey for marsupial lions, thylacines, and other large carnivores (or scavengers) of their time—all are features which are likely to lead to good representation in the fossil record.

In spite of their commonness, or perhaps partly because of it, our knowledge of their taxonomy is more confused than that of other groups and it is clear that Simpson's (1930, p. 69) hope that this state of affairs would soon be corrected has not yet been fulfilled. The confusion is the result of factors, usual in palaeontology, which are

- (a) the uncertainty of generic limits
- (b) poorly studied subjective synonymy between named species and poorly stated species limits, and
- (c) generally unknown temporal relations between the named species.

#### Generic classification

Since almost all fossil Macropodidae are Pleistocene, it is not unreasonable to suppose that the generic limits of the modern Macropodidae will be applicable except in a few cases where whole genera have become extinct as has happened in the Sthenurinae where both *Sthenurus* and *Procoptodon* are no longer extant. However, not only has the generic classification of fossil kangaroos always lagged behind that of modern kangaroos and wallabies, but generic limits among modern Macropodidae are still undecided (see Ride 1962a for a statement of the positions taken by various authorities in modern times). Fortunately, taxonomic activity is such that investigations which are currently in progress of

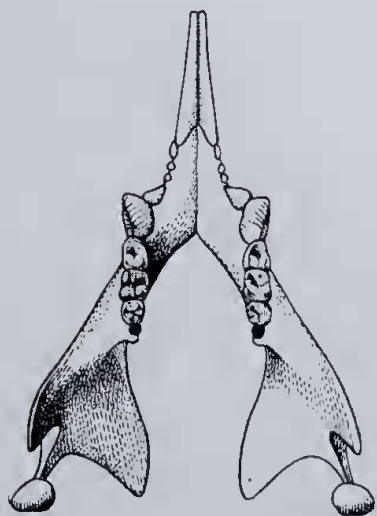
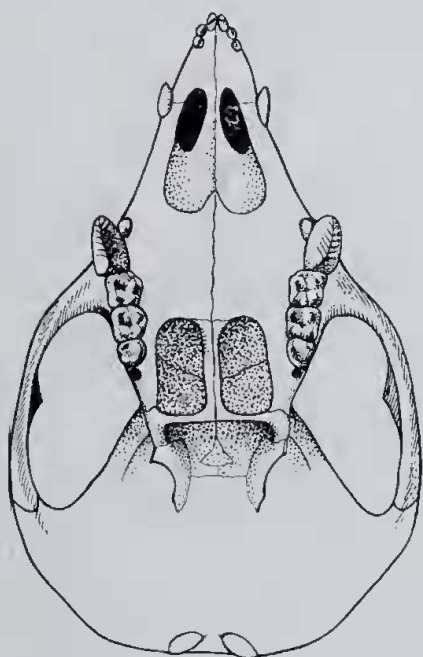


Fig. 11.—*Burramys parvus*. Occlusal views of restored cranium and mandible (from Ride 1956), x 2.5.

behaviour, chromosomes, blood sera, soft part anatomy, bone, and dentition, will greatly advance our interpretation during the next decade, and then the taxonomist of fossil kangaroos will be in a much better position to produce a comparable arrangement. At present the taxonomist of fossil kangaroos can only place his generic limits by interpreting a limited and imperfect number of characters and without much help from neontological studies which can often lead to much more meaningful interpretation.

Today, the area of most confusion among modern animals is that surrounding the limits of *Macropus*, *Megaleia*, *Osphranter*, *Wallabia* and the other middle-sized wallabies. This confusion is made worse for the taxonomist of modern Macropodidae by the uncertain relationship between the type species of *Wallabia* (*W. bicolor*) and the group of large fossil wallabies called *Protemnodon*; Stirton (1963) has shown that these large fossil wallabies are distinctive, but it is still not clear whether the characters in which they differ from some of the modern wallabies are merely expressions of size increase which alone is scarcely a character upon which to separate genera. The position is made even more unstable by the knowledge that *Wallabia bicolor* differs very greatly in chromosome morphology from other modern middle-sized wallabies and is scarcely likely to be congeneric with them; these may require yet another generic name. At present we can only await the result of further studies to clarify the position; in the meantime it would seem very reasonable for the neontologist to do as most authors do and deliberately ignore the fossils, and also the differences between *Wallabia bicolor* and other wallabies, and use the name *Wallabia* for this group.

It is probable that this deliberate cleavage between neontological classification and palaeontology is desirable for stability in the names of fossils as well. At present the incomplete nature of most material of fossil species precludes its identification with genera which are established by the neontologist upon the characters provided by more complete material. Thus, while taxonomists of modern animals find little difficulty in deciding whether or not a species, or population, belongs with one or other of the hypsodont kangaroos *Macropus* or *Megaleia*, some fossil species can scarcely be so assigned; therefore the taxonomist of fossil kangaroos is forced to adopt wider limits and include both genera together. Since these limits imply equivalence with modern genera to zoogeographers and others, much might be said for the abandonment by palaeontologists of generic names of Macropodidae which possess living animals for type species and fall back on the use of purely fossil species concepts which will be dictated by the nature of the material. Thus, kangaroos with high crowned molars with rapid dental progression and premolars which are early shed (see below), would be distinguished from forms with relatively low crowned molars and with tenacious premolars; these latter forms could be further subdivided into those very large forms with very great premolars which are never shed, and those smaller forms which shed even their premolars in extreme old age.

The most recent classification of the species of fossil kangaroos (Simpson 1930) was regarded by its author as unsatisfactory. In it some species are obviously greatly lumped while others are in monotypic genera which are clearly not comparable. This is a legacy which is the result of the alternating actions of describers (who split) and synthesizers (who lumped). We are now in a describing phase with descriptions being added to a lumped classification, a classification which is due in greatest part to Owen, De Vis, and Lydekker.

The history of this sequence commenced in 1838. Prior to 1863, the date of completion of Gould's Mammals of Australia, the taxonomy of modern Macropodidae as generally accepted in Britain (see Owen 1840, and Waterhouse 1846) was uncomplicated containing only three genera *Macropus*, *Hypsiprymnus* (= *Potorous*) and *Dendrolagus*. The five species described by Owen prior to 1873 (i.e. 1838-1859) were all included in the first two of these. Of the remaining sixteen species which he described (i.e. 1873-1877), one was a potoroine which he included in *Betongia* Gray 1837, two were placed in *Osphranter* which had been introduced by Gould, one (*M. ferragus*) was placed in *Macropus*, and the remainder were all placed in six new genera (as well as these, Owen even placed in these new genera two of the five species of his early period and the solitary *Macropus*, i.e. *M. ferragus*, of his later period). Owen thus left twenty-one species distributed between ten genera.

Owen was followed by Lydekker who, in his standard work, the Catalogue of the Fossil Mammalia in the British Museum (Natural History) (1887), placed all of these in the four genera *Macropus*, *Sthenurus*, *Procoptodon*, and *Aepyprymnus* (ignoring the status of *Hypsiprymnus* = *Potorcus*). Since we would remove *Aepyprymnus* today to the Potoroinae and *Sthenurus* and *Procoptodon* to the Sthenurinae, Lydekker actually placed all Macropodinae in the single genus *Macropus*.

De Vis followed him, describing fifteen species of Macropodidae and three new genera between 1883 and 1895. These three new genera had one species each and of them one, *Triclis* (= *Propleopus*), is a potoroine while the other two are fragments generically not determinable. The remainder of his species were described as belonging to *Sthenurus* (in which he included *Procoptodon*), *Macropus* which he confined to the hypsodont kangaroos, and *Halmaturus* a name which he applied (actually, misapplied, following others) to all the remainder.

The most recent complete revision is Simpson's (1930) Post-Mesozoic Marsupialia, and again the synthesis produced a lumped taxonomy. In effect Simpson returned to the concepts of Lydekker, except that he recognized *Protemnodon* Owen, and placed all the *Halmaturus* fossils of De Vis into *Macropus*.

Today we have thus a classification of fossil kangaroos which is excessively lumped when compared with the generic classification of Recent forms. The only Macropodinae outside *Macropus* are *Brachalletes* De Vis and *Synaptodon* De Vis which are probably not determinable, and *Protemnodon* which is confined to an



uncertain number of very large, large-premolar fossil wallabies; and the newly described *Prionotemnus* Stirton (1955) which has not yet been satisfactorily compared with any other genera.

### Structure and Terminology in Macropodidae

Descriptions of fossil macropod species are particularly difficult to evaluate and this leads to uncertainty in subjective synonymy. In the main these descriptive complications are due to nature of the macropod skull and dentition and in particular to its ontogenetic processes, but they are also unduly confused at present by the existence of more than one set of dental terminology.

Like the Phalangeridae from which they were clearly derived, the Macropodidae possess quadricuspid molars but, unlike most of them, these are often further complicated by the development of lophs, links, and folds of enamel which increase their efficiency as grinders. Canines are generally absent and, as in Phalangeridae, incisors are reduced to three above and a single pair below. However, the acquisition of a grazing habit and the development of elongate sectorials has resulted in the elaboration of the masseteric musculature and in particular a masseteric foramen is developed in the mandible (see Ride 1959). Premolars have been reduced to two only in the permanent series and with this has come a unique sequence of replacement in which the most posterior permanent premolar supplants not only its milk predecessor but also the preceding permanent tooth. Since both permanent teeth are elaborate sectorials (or are derived from them) while the milk tooth is a molariform tooth, the macropod tooththrow always comprises a sectorial followed by a row of molariform teeth. In *Hypsiprymnodon* alone of the Macropodidae both permanent premolars have a brief coexistence in fully erupted state (Woods 1960, Ride 1961). Complexity does not end here, however, because in many Macropodidae the molar tooth-row moves bodily forward during the life of the animal (fig. 12) with the result that the position of various teeth in relation to various cranial features are progressively altered, and even the angles of the various teeth and their longitudinal dimensions change. Further, the permanent premolar (and even succeeding molars) may be shed from the front of the jaws as in the great kangaroos, or molars

may be impacted and shed laterally from behind the permanent premolar as in some wallabies. Since characters such as the relative positions of teeth to bony processes, and even the degrees of development of these in Macropodidae, are so very dependent upon ontogenetic stages, they are very difficult to interpret when they are used in descriptions which involve insufficient material to establish the various developmental sequences.

Differences in the terminology of premolars applied by two schools of dental nomenclature are nowhere more obvious than in the taxonomy of Macropodidae since the characters of the two permanent premolars are often diagnostic. One school holds that since more than three permanent premolars have not been discovered in known Marsupialia these should be numbered 1, 2, 3. The other school (of which I am one, and I have consistently applied the 1, 3, 4 nomenclature in this review) notes that since Marsupialia and Eutheria are probably monophyletic and that Eutheria possess up to four premolars, known Marsupialia have probably lost one. The last tooth with a predecessor (i.e., the most posterior premolar) is always in contact with the first molar (unless, as in some Dasyuridae, it is absent), accordingly this is called 4 and is regarded as homologous with the fourth premolar of Eutheria and Triconodonta. This conclusion was adopted by Thomas whose 1888 Catalogue forms the foundation of all modern taxonomic work on marsupials; by Lydekker whose Catalogue (1887) summarizes and synthesizes Richard Owen's work; by H. H. Finlayson, E. Le G. Troughton and G. H. H. Tate whose monographs on Australian Marsupialia together make up the greater part of all modern taxonomic work on this group; and by C. W. De Vis who, second only to Richard Owen, was responsible for the greater part of the descriptive literature on fossil Macropodidae. The other two premolars are called by this school P3 and P1 in accordance with the observation that there is most usually a gap between the most anterior and the intermediate premolars.

While two schools of premolar terminology have been in existence for some time (the literature of American marsupials generally applies the P1, 2, 3 terminology) a second school of incisor terminology has only lately arisen. It was introduced by Stirton (1955) who used

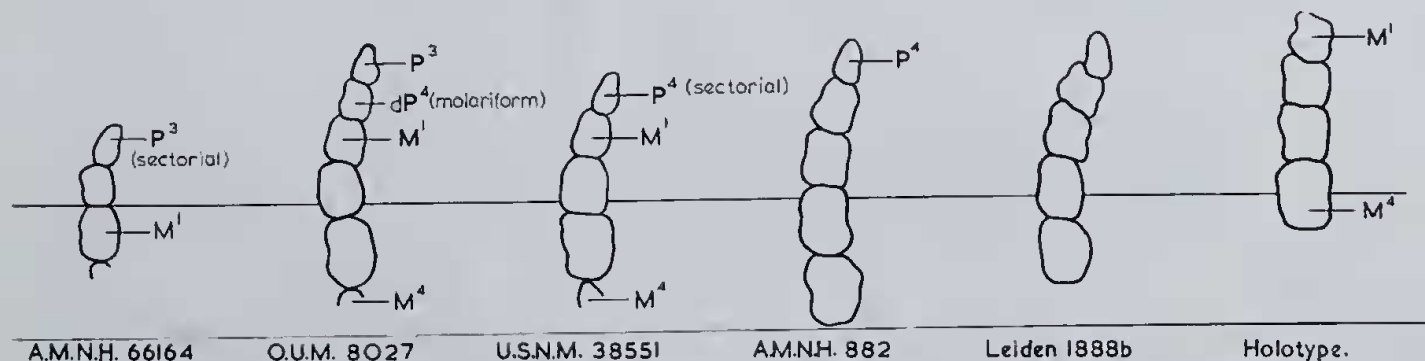


Fig. 12.—The succession and forward movement of cheek-teeth of Macropodidae illustrated by the modern wallaby *Protomnodon parma*. The transverse line indicates the position of the tips of the descending zygomatic processes of the maxillae. The youngest individual is on the left, and the oldest is on the right (after Ride 1957).

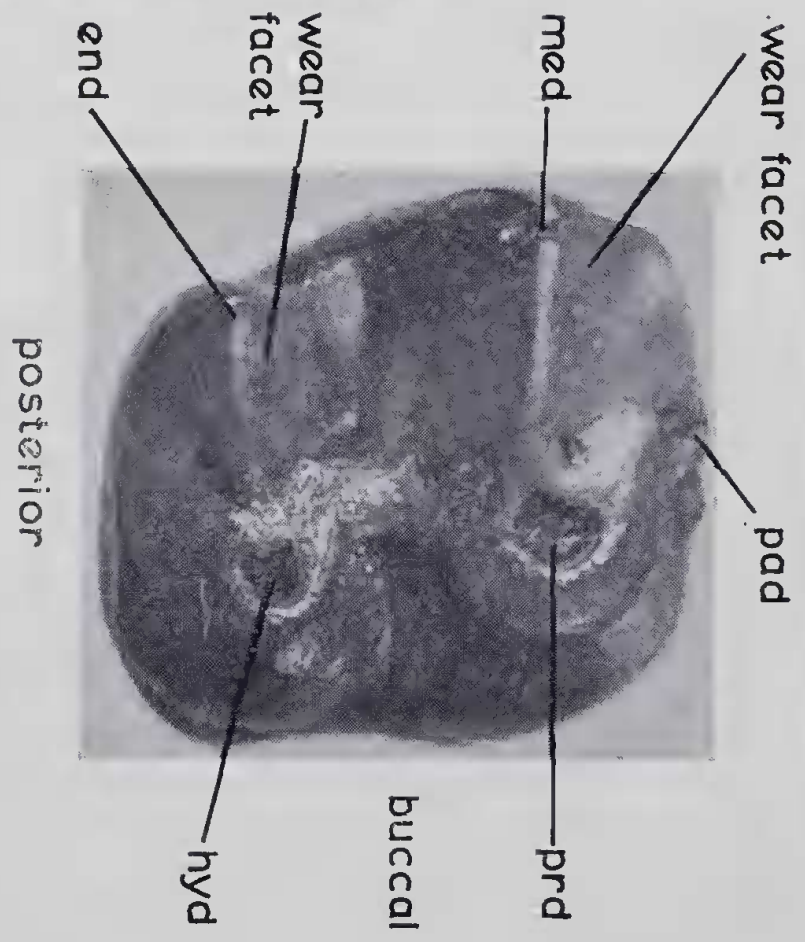
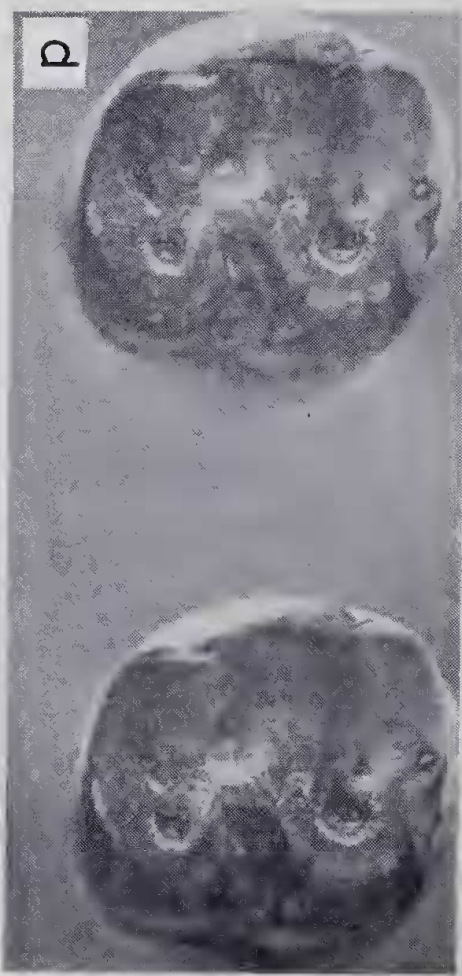
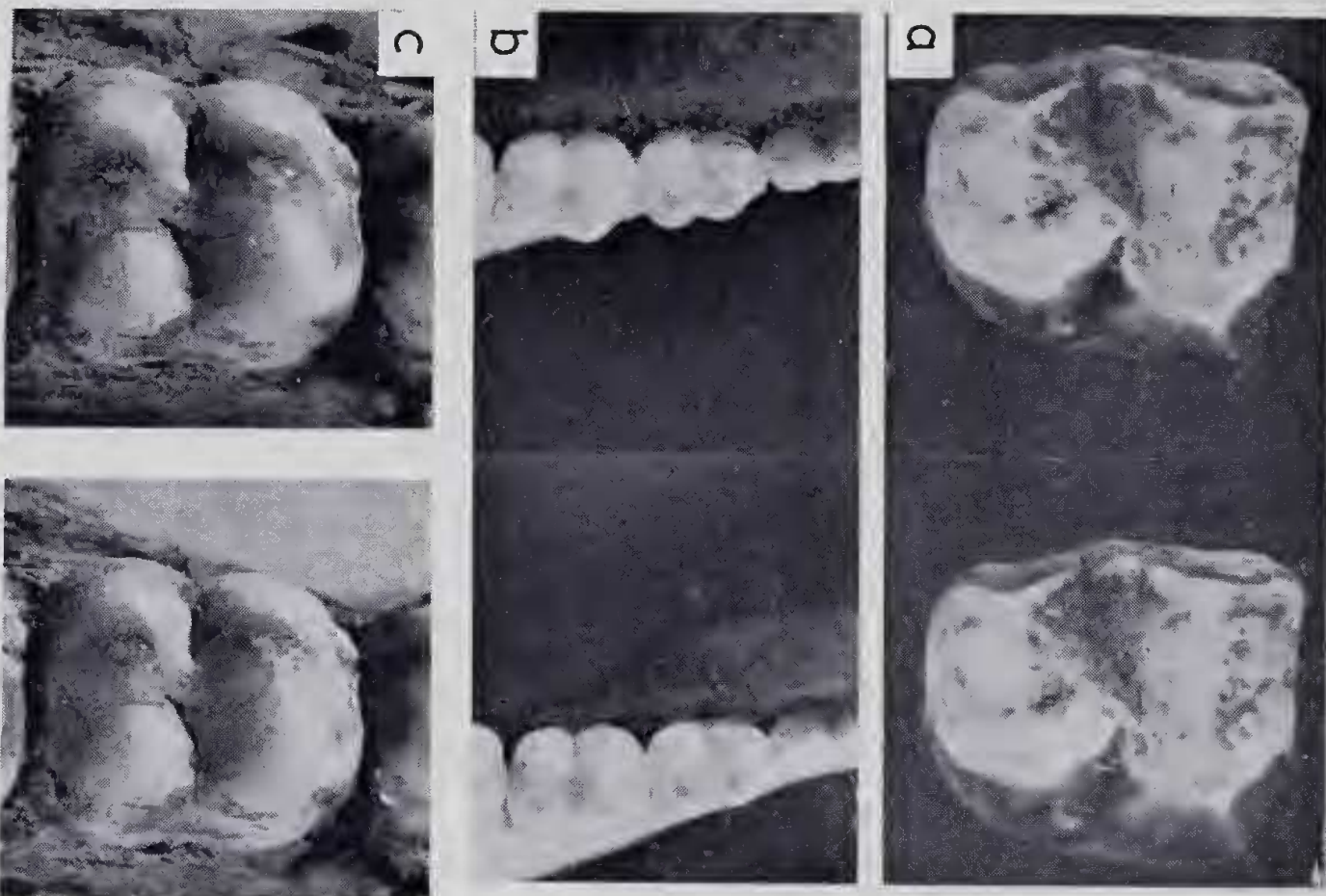


Fig. 13.—The Grange Burn molar, and stereo-pairs of other molar teeth for comparison. (a) *Phalanger ruficaudatus* rt. M<sub>2</sub>. (b) *Poterous gilberti* rt. M<sub>1</sub>. M<sub>2</sub>. (c) *Propitopus oscillans* left M<sub>2</sub> of holotype (photograph by courtesy of Qd Mus.). (d) Grange Burn tooth. Stereorelief and scale not uniform.

the names  $I_2^{2-4}$  for the upper incisors and  $I_1$  for the lower, in place of the usual  $I_1^{2-3}$  and  $I_1$ , stating at the time that this was based upon the assumption that the primitive incisor formula in marsupials is  $\frac{1 \cdot 2 \cdot 3 \cdot 4 \cdot 5}{1 \cdot 2 \cdot 3 \cdot 4 \cdot 5}$  and

that the remaining incisors of the Macropodidae are  $\frac{0 \cdot 2 \cdot 3 \cdot 4 \cdot 0}{0 \cdot 2 \cdot 0 \cdot 0 \cdot 0}$ . Stirton has since

(1963) abandoned this terminology, but Marcus (1962) has adopted it. I have reviewed (1962, pp. 297, 8) the embryological evidence for the primitive incisor formula in marsupials and there is little doubt that evidence exists which suggests that the formula is at least six in the upper jaw. It is also likely that the diprotodont lower incisors are the third or fourth teeth of the series. In spite of this, I would not at present advocate the introduction of a further incisor terminology to upset that which is in almost universal use until the fossils are found which demand it.

#### Phyletic lines in Macropodidae

Today, there appear to be three phyletic lines of Macropodidae. One of these, the Potoroinae (Hypsiprymnodontinae and Potoroinae of earlier authors—see Woods 1960) appears to be an early offshoot combining a number of primitive characters (such as a hallux and simple alimentary canal in *Hyprispyrnodon*, and relatively simple molars in most of the group), with a number of extreme specializations (like anterior vaginal expansions, plagiaulacoid premolars, and enormous masseteric canals. See Pearson 1949, Woods 1960, Ride 1961).

The most modern of the offshoots from the main stem is the Sthenurinae. These are secondarily adapted for browsing from the main grazing line (see Ride 1959) and culminate in *Procoptodon* with deep, heavy mandibular rami, broad crushing premolars, wide highly "ornamented" molars, erect lower incisors, reduced upper incisors, elongate descending zygomatic processes of the premaxillae, and a coossified mandibular symphysis.

The Macropodinae are the stem forms of the radiation. At their most highly evolved they are supremely modified for grazing and swift cursorial (saltatory) existence. However, within the Macropodinae numbers of different kinds of modification are visible; some of them are small animals with scarcely any of the grazing modifications we associate with the group (e.g., *Lagostrophus*, see Thomas 1887) while others are large grazers which place almost no dependence upon their sectorial premolars and shed them early, meeting all their masticatory requirements with a rapidly progressing molar row. In these "end forms" molars are hypsodont to meet the abrasive effects of silica-containing grasses and, like those of their eutherian counterparts, lophodont molars have links which increase the efficiency of their grinding surfaces. Some Macropodinae have enlarged sectorials almost to the extent of the Potoroinae. In the past some of these forms with large sectorials were very large (e.g., *Protemnodon*) but today

they are generally of moderate size and include the forest and thicket dwelling wallabies and tree-kangaroos (*Wallabia bicolor*, *Dorcopsis*, *Dorcopsulus* and *Dendrolagus*); these Macropodinae possess simpler molars than their grazing adapted relatives.

Until recently, *Palorchestes* was believed to be a giant kangaroo, however revision by Woods (1958) has shown unequivocally that this genus represents a slenderly built line of Diprotodontidae which possibly bears to the heavily built Diprotodontinae the same relationship as the eutherian tapirs do to the rhinoceroses.

At present it is not possible to provide a detailed arrangement of fossil kangaroos because proper comparison has yet to be made between the confused samples described from the various strata of the Darling Downs and the various species described by Owen. Revisions of fossil taxa of Macropodidae, or parts of them which have been completed in recent years are of *Sthenurus* (Bartholomai 1963, Marcus 1962), *Protemnodon* (Stirton 1963), *Propleopus* (Woods 1960). However, one form does require special comment because it has to date been referred to the Phalangeridae and (as a cuscus) has even taken its place in palaeoclimatic speculation (Gill 1957, p. 159; 1961, p. 336). This is the fossil tooth from Grange Burn.

#### The Grange Burn Potoroo

The Grange Burn Potoroo is one of the most tantalizing of fossils. It is possibly Pliocene and comprises a solitary enamel cap of a macropod second or third right lower molar (Nat. Mus. Vict. No. P 15777). It was collected by Edmund D. Gill, of the National Museum, in the bank of Grange Burn, one mile upstream from Forsyth's Bank, near Hamilton, Victoria. It came from a fossil podsol 6 ins. below basalt, where the Burn flows off the basalt on to Tertiary rocks. Gill (1953a, 1957) regarded the tooth as being cuscus-like and Stirton (1957) agreed, comparing it with the second and third right upper molars of *Phalanger maculatus* and *Ph. orientalis*. He noted that the main difference between the fossil and the cuscuses was that the fossil was larger, more elongate, and possessed a "prominent median lingual inflection"; he regarded the tooth as being much too worn to show any indication of the crenulated surface typical of the *Phalanger* tooth.

Comparison with a wider range of diprotodonts reveals that the tooth is undoubtedly that of a potoroine. It is inseparable in general morphology, positions of wear facets, and patterns of exposed dentine from modern *Potorous* but it is very much larger having about twice the linear dimensions of equivalent teeth of *P. gilberti*. It is as distinct from the other potoroines *Bettongia*, *Caloprymnus*, and *Aepyprymnus* in size as it is from *Potorous*, but detailed comparison of cusp patterns with these has not been made. It is distinguishable from *Propleopus* in its smaller size, more acute lingual cusps, complete absence of a median longitudinal valley, and in its inequality between anterior and posterior transverse dimensions.

The fossil tooth (fig. 13) has four cusps; two of these, the protoconid and hypoconid, are low in relief and rounded (protocone and hypocone of Stirton 1957, p. 122) while the other two, the metaconid and entoconid, are high and angular (paracone and metacone of Stirton). As measured from the base of the enamel to the tip of the cusp, only the protoconid is really lower than the others (prd 3.3 mm, med 3.9 mm, hyd 3.8 mm, end 3.9 mm), but the relief of the occlusal surface is such that the two sharply angled lingual cusps appear to stand above their rounded buccal counterparts. There are two clearly-defined flat areas at opposite ends of the periphery of the tooth which are, without doubt, areas of contact with adjacent teeth in the tooth-row. Of these, the anterior is broadest and from its buccal edge a broad, shallow channel rises onto the occlusal surface of the tooth to separate off a small "antero basal cingulum" (more properly this channel is the remnant of the entrance to the trigonid basin between protoconid and the almost completely reduced paraconid, see Ride 1961). Dentine is exposed in small sub-circular areas at the tips of the buccal cusps and there are also three smaller dark patches in other places on the occlusal surface which almost certainly mark the presence of fissures or pits in the enamel; the most prominent of these lies postero-buccal to the entoconid and represents the posterior part of the talonid basin (see Ride 1961, pp. 56, 7).

The occlusal surface of the tooth shows only moderate wear; the posterior surfaces of the semi-lophids (*i.e.* the areas which lie posterior to the transverse ridges which run from the acute metaconid to the rounded protoconid, and from the acute entoconid to the hypoconid) are covered with enamel which has a faintly pitted surface which is obviously quite unworn since it lacks facets, or the microscopic scratches which are typical of dentally abraded surfaces. However, in contrast, the anterobuccal faces of the metaconid and entoconid have well marked wear facets with pronounced microgrooves; these wear facets have not passed through the enamel into the dentine beneath. Wear through to the dentine is only present on the tips of the two buccal cusps; here, more or less circular areas of dentine are exposed. The rounded buccal shoulders of these cusps are also well-marked with microgrooves and in particular, these are concentrated in slight facets anterobuccal and posterobuccal to each cusp.

The length of the tooth from anterior to posterior contact areas is 8.3 mm, breadth at level of anterior cusps 7.8 mm, and breadth at level of posterior cusps 6.4 mm.

Since other authors have regarded this tooth as being most like a right upper molar of *Phalanger* while I regard it as being a right lower molar of *Potorous*, differences between these teeth are rather important (fig. 13a, b) and are tabulated here.

Rt M<sup>2</sup> *Phalanger* (*nudicaudatus* and *maculatus*)

1. All cusps sharply angular.
2. Wear facets on posterior faces of semi-lophids.

3. When wear is at the stage where dentine shows through the tips of lingual cusps only and not through the buccal cusps, the anterior faces of the semi-lophids are deeply ridged with crenulated enamel.
4. As the tooth wears, the area of exposed dentine spreads anteriorly and posteriorly from the tips of the lingual cusps to form two Vs along the antero-postero ridges. After this stage it begins to spread buccalwards along the transverse ridges of the semi-lophids.
5. The antero lingual face of the protocone is flattened and facet-like. There is no antero basal cingulum.
6. There is no fissure posterior to the transverse ridge between hypocone and metacone.

Rt M<sub>2</sub> *Potorous* (*gilberti*)

1. Lingual cusps angular, buccal cusps rounded.
2. Wear facets on anterior faces of semi-lophids.
3. When only two of the cusps (*i.e.* the low rounded buccal cusps) show exposed dentine there is no crenulated enamel on any faces of the tooth.
4. As the tooth wears the area of exposed dentine at the tips of the two rounded buccal cusps spreads transversely across the tooth, not anteroposteriorly until after the pairs of transversely placed cusps become joined.
5. The antero buccal face of the protoconid carries a broad shallow channel which opens out onto the occlusal face of the tooth, separating a small "antero basal cingulum".
6. The posterior part of the basin of the talonid is represented by a fissure in the enamel, posterior to the transverse ridge between the posterior cusps (end & hyd).

The Grange Burn fossil possesses all the characters of the *Potorous* molar and none of those of *Phalanger*.

The only fossil potoroine which approaches the Grange Burn fossil in size is *Propleopus oscillans*. Woods (1960, p. 201) gives dimensions of the lower molars of two specimens of *P. oscillans* as being M<sub>1</sub> 9.5 x 8.7 and 9.3 x 9.2, M<sub>2</sub> 10.8 x 9.8 and 10.1 x 10.0, M<sub>3</sub> 11.2 x 10.3 and 10.7 x 10.2 mm; the Grange Burn fossil measures 8.3 x 7.8 mm. There are also considerable resemblances in general morphology. Comparison with stereoscopic pairs provided through the kindness of Mr. J. T. Woods (fig. 13c) reveals that the *Propleopus* lower molar differs in having more rounded lingual cusps, a more pronounced median longitudinal valley (defined Ride 1961, p. 56, under M<sub>2</sub>) which is completely lacking in the Grange Burn fossil but visible in all molars of the holotype of *P. oscillans*. The molars of *P. oscillans* also seem much more square (except M<sub>1</sub> and M<sub>4</sub> which the Grange Burn fossil cannot be: it is not M<sub>1</sub> because the anterior moiety is broader than the posterior moiety and is not M<sub>4</sub> because there are contact surfaces at both ends of the tooth).

Since the differences between the Grange Burn fossil and *P. oscillans* are slight and are certainly no greater than those between related species in other genera of Macropodidae it is not possible to decide with any degree of certainty whether this single tooth should be placed in *Propleopus* on grounds of size, or whether it should be regarded as a gigantic *Potorous* on grounds of morphological similarity. It seems safest to conclude, for the present, that it is a potoroine and leave naming it until further material is discovered. The present tooth contains sufficient features to be certain that the species is new, but it will require the discovery of a fourth molar or a premolar to provide sufficient diagnostic characters to name the genus.

## Diprotodontidae Gill, 1872

The Diprotodontidae are the giants of the Australian fossil record. These great quadrupedal herbivores are well represented in the fossil record as far back as the Miocene. Unfortunately, there has been no modern synthesis of the group (which is now known to contain two divergent phyla, the lightly built *Palorchestes*-like forms and the more typical diprotodontids) and the status of a number of the species, e.g. *D. minor*, *D. bennetti*, *D. longiceps*, is not clear from the literature. De Vis (1891b) provides a key to the genera; he also considers that *Sceparnodon* probably belongs here (see under *Vombatidae*)\*.

The most valuable statements of the temporal distribution of diprotodontids are in surveys by Woods (1960a, 1962) and data selected from these are tabulated below. In this table many formations and localities are omitted to avoid duplication but sufficient are given to indicate the diprotodontid faunal associations, and the distributions of various species. As Woods suggests, it seems likely that Diprotodontidae will prove to be stratigraphically important.

Age	Formation, etc.	Species
Recent ....	Tartarua culture BP 6.570	<i>Diprotodon optatum</i>
Pleistocene	Mowbray Swamp, Tas.	<i>Nototherium tasmanicum</i> <i>N. mitchelli</i>
	Diprotodon Beds, Darling Downs, Qd.	<i>Diprotodon optatum</i> <i>Nototherium mitchelli</i> <i>Palorchestes azael</i> <i>Euowenia robusta</i>
Pliocene	Otibanda Lake Beds, N.G.	<i>Nototherium watutense</i> (? = <i>Mensiscolophus</i> )
	Chinchilla Sand, Darling Downs, Qd.	<i>Euowenia grata</i> <i>Euryzygoma dunense</i> <i>Palorchestes parvus</i> <i>Diprotodon</i> sp. (Woods 1962, p. 46)
	Mampurwordin Sands, S.A.	<i>Mensiscolophus mawsoni</i> <i>Euowenia</i> -like form
Miocene	Cheltenhamian Stage, Vic.	<i>Nototherium</i> (premolar figd Stirton 1957 see Woods 1962, p. 45) Diprotodontidae. Maxillary and mandibular fragments
	Etadunna Fm., S.A.	Small diprotodontid with ? <i>Palorchestine</i> affinities (Stirton <i>et al</i> 1961, pp. 36, 7)

Note: The sequence of the formations within each age does not necessarily indicate temporal succession.

The Otibanda Lake Beds were formerly thought to be Pleistocene but parts of them are probably Upper Pliocene. Stirton (1963, footnote 10 p. 144) gives a K. A. date of 4.5 million years for pyroclastics associated with them.

## Vombatidae Iredale & Troughton, 1934.

The origin of wombats is unknown although their diprotodonty and syndactyly clearly indicate that they are Diprotodonta. Dental characters are aberrant in them and give little real clue to their relationships with other families in the order. Various attempts have

\* Since this address was given Stephenson (1963) has endorsed this conclusion and has, in addition, described a new species and genus of diprotodontid, *Diarcodon parvus*.

been made to elicit affinities from these and other anatomical features, and Tate (1951, p. 3) has reviewed this work.

No Tertiary wombats have yet been described and no fossils are reported as having been collected in the various deposits of this age investigated by Stirton in Central Australia or Victoria. Woods lists none from the Chinchilla Sand (Woods 1960a, 1962) nor does De Vis (1891) although the general term "Darling Downs" which he uses for Queensland wombats may include this Pliocene formation.

The most recent revision of the wombats is by Tate (1951) who dealt with both fossil and recent forms. This work, when taken together with Lydekker's (1887) catalogue (to which Tate does not refer), provides a very adequate summary of present knowledge of the fossils. However these two works differ slightly in arrangement. Lydekker's list is most useful in providing concise descriptions and a synoptic view of Owen's fossil species, but it should be read in the light of De Vis' further revision of the status of the species *P. mitchelli* and *P. thomsoni* (De Vis 1891). In his arrangement, Lydekker adopts a classification which is that used for modern wombats today, i.e. he recognizes two main kinds of normal-sized wombat (the plains-dwelling *Lasiorhinus* wombats and the *Vombatus* species of the more densely timbered country) although of course he uses only the name *Phascolomys* which was then in general use for them all. He employs *Phascolonus* for the Pleistocene Giant Wombat.

Of the fossil wombats known today, Lydekker's revision omits only *P. hacketti* Glauert, 1910, *P. angustidens* De Vis, 1891 (which were described since) and *P. pliocenensis* McCoy, 1874 (which was not noticed by him). Tate places *P. hacketti* and *P. pliocenensis* with *Vombatus*, and *P. angustidens* with *Lasiorhinus*. Both Tate and Lydekker exclude *P. curvirostris* from these two groups; Lydekker regarding it as *incertae sedis*, while Tate creates a new genus, *Ramsayia*, for it. Tate regards the position of *P. medius* Owen and *P. magnus* Owen as uncertain. Lydekker includes them in the *Vombatus* group.

*Phascolonus*, the genus of Giant Wombats, is universally accepted and is now known from very much better material than Lydekker or Owen possessed; this is from Lake Calabonna (Stirling 1913). The genus *Sceparnodon* is conventionally placed in synonymy with *Phascolonus*, but with some reserve (Tate 1951, p. 12) because of De Vis' (1891a) strong arguments that these were not synonymous and moreover were not even closely related. He regarded *Sceparnodon* as being diprotodontid (see above under Diprotodontidae).

## MARSUPIALIA *incertae sedis*

### Notoryctidae Ogilby, 1892.

*Notoryctes*, the marsupial mole, is unknown as a fossil and it is so highly specialized in dentition, skull structure, and limb structure that arguments as to its affinities which are based upon these features can only produce tentative results. It is usual to follow Stirling's (1891) original conclusions and relate it to the

Dasyuridae (see Wood Jones 1923, and Simpson 1945). However, Bensley (1903, p. 173) regarded the foot structure of *Notoryctes* as being derived from "one of ordinary phalangerine type" and its dentition as having been "so modified away from the usual dasyurid and peramelid type that it does not present any of the special characters which distinguish the dentition of these two families" (Bensley 1903, p. 117). Accordingly he placed *Notoryctes* (p. 210) in the "polyprotodont syndactyla" with the Peramelidae. Cabrera (1919, p. 90) followed Bensley. Van der Klaauw (1931, p. 254) has pointed out that the structure of the tympanic in *Notoryctes* agrees more with Diprotodonta than with other marsupials. Some authors (e.g. Troughton 1959, p. 75) have preferred to remain uncommitted and, in view of the introduction of ordinal classification here, it seems wisest to follow them.

### The Australian Radiation—Origin, Isolation and Drift.

The Australian radiation, by comparison with mammal radiations of other inhabitable land masses, is unbalanced in the degree in which various major taxa of terrestrial mammals (and in particular Cohorts) are represented in it. Thus, with the exception of the dingo (an obviously Pleistocene, or Recent, introduction), Ferungulata are absent but represented in all others; Unguiculata (except for flying forms such as bats) are absent but present in all others; and Glires, while present, are confined to representation from a single suborder of Rodentia (and a single family of these) when other continents have representatives of both orders and all suborders.

The explanation of this can only be that the Australian Continent has been through a very long period of isolation which has lasted through much of the Age of Mammals. However, in this isolation, Australia has developed a wide and comprehensively diversified mammalian fauna, almost entirely marsupial, which has paralleled the mixed marsupial and eutherian radiation of South America, and pure eutherian radiations of other continents, in almost all of the kinds of niche available to mammals. Thus, while in South America the marsupials provided the carnivorous predators and smaller insectivores and carnivores, the archaic ungulates of that continent provided the herbivores (see Simpson 1950). In Australia all three main adaptive avenues were filled with marsupials. Moreover, they were not interrupted by invasions of similarly adapted mammals from outside during this period (or if they were the invaders were repelled leaving no trace).

During the early part of this century many responsible zoologists believed that the long isolation of Australia, taken together with the fact that the greater component of the Australian fauna was marsupial and similar to that of South America, could best be explained by the theory of Continental Drift. Further, palaeontologists working on South American marsupials argued for the existence of special relationships between separate parts of the South American Marsupial fauna and parts of

the Australian fauna; in particular between *Thylacinus* and Borhyaenidae, and between Diprotodonta and Paucituberculata. I have reviewed this work, and that of others, and conclude that these relationships cannot be supported (Ride 1962).

Most zoologists today believe that an alternative explanation, due principally to W. D. Matthew and G. G. Simpson, is more reasonable; this states that Australia has been no more isolated during the whole of the Age of Mammals than it is today and during this period entry to it has been by a combination of chance and rafting ability across the water gaps of the Malaysian archipelago. Thus, it is the effect of chance which has led to the imbalance of the Australian fauna. In contrast, many botanists (see Good 1963, but also see Burbidge 1960 p. 156 for expressions of reserve) would not agree with this conclusion and still hold to the theory of Continental Drift, observing that the short distance across Torres Straits marks a greater floral discontinuity than any similar distance on the earth's surface and moreover floral continuity with the archipelago occurs through New Britain, the New Hebrides and New Caledonia and, allowing for differences of latitude, even to New Zealand; they conclude therefore that the floral discontinuity can best be explained by the hypothesis that the gap between Australia and New Guinea has only become narrowed by the northward drift of the Australian continent.

In recent years geophysical work on palaeomagnetism supported by data of palaeoclimatology (see Runcorn 1962, Nairn 1961) have made it reasonably certain that Continental Drift has occurred. The direction of the magnetic field of rocks of known age on a single continent can be plotted to give a polar wandering curve for that continent which probably indicates the positions of the magnetic poles at various ages relative to it. It is now known that polar wandering curves of the various continents do not agree and that the pole positions given by various continents for any particular age can only be made to agree by displacing the continents relative to each other, i.e., by "drifting" them. Until very recently, it was not known whether Continental Drift as postulated from these data occurred late enough in time for it to effect the composition of the Australian Mammal fauna. However, the work of Irving *et al* (1963) have made it abundantly clear that Australia only achieved its present latitude during the late Tertiary and that since the Mesozoic it has been moving slowly northwards across what is now the Southern Ocean.

It seems that as biologists we are now in the fortunate position of having a very reasonable working hypothesis which has been erected solely on non-biological data and which we can now test by biological observation. Fossil marsupials do not yet help us: such marsupials as have yet been found in New Guinea are Pleistocene and upper Pliocene (Stirton 1963, Woods 1962) while the distribution of modern marsupials in New Guinea and the adjacent islands is entirely consistent with its being the product of alterations in Pleistocene sea level, and

even through chance distribution across very short water barriers over a very short space of time.

On the other hand a very wide water gap between Australia and Asia during much of the Tertiary is supported by the apparent lack of success enjoyed by non-marsupial invaders before at least the Miocene (the Muridae first appear in the fossil record in the Pliocene of Europe and Asia). During the early Tertiary, Asia certainly possessed such highly efficient short water-barrier crossers as Primates, Insectivora, Scuriomorpha, Hystricomorpha, etc. After all, even elephants succeeded in crossing into Celebes and across Wallace's Line into Flores during the Pleistocene (Hooijer 1962).

#### Added in Proof

Since this address was submitted for publication, a number of articles with important bearing on it have come to my notice. These are by Chow (1963), Hofer (1952), Hooijer (1964), Kean, Marryatt & Carroll (1964), Macintosh & Mahoney (1964), Mahoney (1964), Mills (1964), and Stephenson (1964).

The nature and character of ancestral marsupials (see Fig. 1 and under Phylogeny) are clarified by J. R. E. Mills whose work (1964, *Proc. Linn. Soc. Lond.*, Vol. 175, pp. 117-133) would indicate common ancestry of Eutheria and Marsupialia among the Amphitheriidae of the Upper Jurassic. Formerly, inadequate material of Pantotheria led Simpson (1945, pp. 169, 70) to state that "Despite a general resemblance, the dental differences in detail [between pantotheres, marsupials and eutherians] are great, and various attempts to homologize molar cusps or to specify closer affinities are so contradictory and hypothetical as to provide no worth while data for taxonomy." Now, however, newly prepared specimens of *Peramus* and *Amphitherium* from the Upper Jurassic suggest that the relationship is closer than hitherto suspected and that the molar pattern of Amphitheriidae (in which Mills includes *Peramus*) is well on the way to the tribosphenic condition characteristic of both marsupial and placental lines in the Upper Cretaceous. Mills is of the opinion that, on purely dental evidence, the division between marsupial and placental could date from this stage. In connection with marsupial dental homologies (see under Macropodidae—Structure and Terminology) it is of interest to note that specimens of *Peramus* examined by Mills possess a canine, four premolars, and four molars; specimens of *Amphitherium* also possess four premolars and five molars, although Mills notes that up to seven molars are known in specimens not seen by him.

R. I. Kean, R. G. Marryatt & A. L. K. Carroll (1964, *Aust. J. Zool.*, Vol. 12, pp. 18-41) have also added data relevant to Kean's earlier argument that the marsupial female urinogenital system is derived from the eutherian condition. They report the presence of epithelial cells lining the median "pseudovagina" of a large series of *Trichosurus vulpecula* and conclude that this epithelium acts as a retarding influence in the closure of the canal after parturition; they are of the opinion that this lining is vestigial and

not rudimentary, hence marsupials with a permanently lined, and open, median canal are, in their opinion, primitive.

The taxonomic status of *Dasyurus affinis* (see under Dasyuridae) has been settled by J. A. Mahoney (1964, *Proc. Roy. Soc. Vict.* Vol. 77, pp. 525-533). Both syntypes, in mensuration and morphology, fall within the range of variation of *Dasyurus maculatus*, a modern species.

N. W. G. Macintosh and J. A. Mahoney (1964, *Proc. Roy. Soc. Vict.* Vol. 77 pp. 507-514) have also added to the complexity of the *Thylacinus* problem by recording a small Thylacine molar from Fromm's Landing in the Murray Valley, South Australia. This tooth comes from a horizon dated at between 1806  $\pm$  85 B.C. and 1931  $\pm$  85 B.C. It is the first small *Thylacinus* tooth (the measurement of M<sup>1</sup> pr.-mc. which these authors give is less than any of the south-western cave Thylacines measured by me) to be recorded to the east of the Nullarbor in an area which is otherwise occupied by the larger form. The tooth is also morphologically unusual in that the protocone is divided.

The identity of *Sceparnodon* (see under Vombatidae and Diprotodontidae) has been clarified by N. G. Stephenson (1964, *Proc. zool. Soc. Lond.* Vol. 142, pp. 537-546). He concludes that it is a member of the Diprotodontidae. Stephenson also expresses the opinion (p. 540) that the only specimen known of *Phascologomys curvirostris* (see under Vombatidae) is possibly a badly eroded rostrum of *P. magnus* "or at least of a member of the wombat series of comparable size to this species". Stephenson has also (1963, *Palaeontology* Vol. 6, pp. 615-624) commented on the distinctness of *Sarcophilus laniarius* and *S. harrisi* (see under *S. laniarius*—Dasyuridae); his measurements of two specimens of *lanarius* and of one of *harrisi* (p. 618) do not support differences in size claimed for them by other authors.

Earlier (1962), I had drawn attention to the fact that, in the absence of Asiatic marsupials, the presence of the notoungulate *Palaeostylops* in the Palaeocene of Mongolia was evidence that a migration route between South America and Asia was open in the early Tertiary. Chow Min-Chen (1963, *Scientia Sinica*, Vol. 12, pp. 1889-1893) has now described a possible megalonychoid xenarthran (*Chungchienia sichuanica*) from the Eocene of Honan. Megalonychoids are unknown outside South America until the Pliocene (Simpson 1945, p. 69). D. A. Hooijer (1964, *Zool. Meded.* Vol. 40, pp. 37-44) has published further information on the pygmy stegodont from Flores. He says that it is similar in size to the species known from Celebes but regards it as unlikely that both are conspecific. The material from Flores comprises two milk molars.

Finally, I am indebted to Dr W. D. Turnbull of the Chicago Natural History Museum for bringing to my notice Helmut Hofer's remarkable "Über das gegenwärtige Bild der Evolution der Beuteltiere" (1952, *Zool. Jb. Abt. 2.* Vol. 72, pp. 365-437) and to Mrs. A. Neumann for translating it. While he reviews no original work on Australian fossil marsupials more recent than

that of Wood Jones on *Wynyardia*, Hofer gives much interesting speculation on the origin of the various marsupial phyla and, in particular, he summarizes the work of various German anatomists and embryologists which is not generally known to readers of the more usual literature on Australian marsupials.

Hofer bases most of his speculation and review of American marsupials on the work of Simpson, and of Australian marsupials on Bensley and Tate. He concludes that, despite lack of fossils, dasyurids are certainly derived from didelphoids, and that borhyaenoids are distinct from *Thylacinus*. He regards the perameloids as a very early lateral branch of the south-east Asian or Australian dasyuroid- or didelphoid-like marsupials, paralleling the South American *Caroloameghinia* among didelphoids. The origin of diprotodonty receives particular attention because of Hofer's own interest in masticatory musculature. He regards shortening of the mandible by mutation as a necessary step and cites modern experimental work with dogs to show that such a step is not only possible, but can also be functional. He is of the opinion that this mutation could have been of frequent occurrence among didelphoids and that this has led to the parallel development of diprotodonty in Caenolestoidea and Phalangeoidea. He supports this view with the observation that the sectorial tooth in these groups is not homologous, but this has now lost much of its force as the result of de Paula Couto's work of 1952 (discussed in Ride 1962, p. 295) which has shown that this view of the sectorials is no longer tenable.

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The line drawings in the text are by Miss Rosemary Hunt except where otherwise acknowledged. Photography (other than that by myself) is acknowledged in the text. I am indebted to Miss Helen Williams for her technical assistance.

#### APPENDIX

##### Statistical determination of Subspecies

The granting of subspecific status (and hence trinomial) to populations is arbitrary and depends upon the morphological distinctness of populations as a whole; subspecies may not be wholly definable in absolute terms by the characters of each member. Various authors have discussed the statistics of this (see Amadon 1949, Simpson 1961, p. 174 and Mayr, Linsley & Usinger 1953, p. 143) giving definitions as lenient as that which requires only 75% of individuals of a subspecies to be determinable from 75% of another, to more rigid requirements such as that of Mayr et al. who require 75% of the individuals of one population to differ from 97% of the other (or 90% from 90%) and Amadon who requires 75% to be separable from 99.9% (or 97% from 97%).

Mayr *et al.* propose the use of the statistic Coefficient of Difference (of samples)

$$(CD) \quad \frac{\bar{X}_a - \bar{X}_b}{s_a + s_b} \quad \text{where } \bar{X}_a$$

is the higher of the two sample means and  $s_a$  its standard deviation.

In this the numerator expresses the distance between the observed means and where this is less than the combined standard deviations the value of CD will be less than 1.0. Using this statistic, Mayr *et al.* require a CD value of 1.28 for separation of subspecies and Amadon would require a CD of 1.9.

As pointed out by Amadon, the use of such a calculation takes no account of the probable discrepancy between observed and actual (*i.e.*, population) means and standard deviations. This matters little where samples are large, but in fossil samples where values are frequently very small, account must be taken of it; or at least it should be made more difficult to achieve significance with small samples than with large ones. Therefore I include confidence intervals in the test which I use here in order to relate these sample values to populations. Since the introduction of confidence intervals imposes upper and lower limits, there are two (population) Coefficients of Difference for each set of observations. These are designated  $CD_1$ , and  $CD_2$ .

$$CD_1 = \frac{\left[ \bar{X}_a - t_{n_a} \left( \frac{s_a}{\sqrt{N_a}} \right) \right] - \left[ \bar{X}_b + t_{n_b} \left( \frac{s_b}{\sqrt{N_b}} \right) \right]}{\sqrt{\frac{(N_a - 1) s_a^2}{n_a \chi_{.025}^2} + \frac{(N_b - 1) s_b^2}{n_b \chi_{.025}^2}}}$$



$$CD_2 = \frac{\left[ \bar{X}_a + tn_a \left( \frac{s_a}{\sqrt{N_a}} \right) \right] - \left[ \bar{X}_b - tn_b \left( \frac{s_b}{\sqrt{N_b}} \right) \right]}{\left[ \sqrt{\frac{(N_a - 1) s_a^2}{n_a \chi_{.975}^2}} \right] + \left[ \sqrt{\frac{(N_b - 1) s_b^2}{n_b \chi_{.975}^2}} \right]}$$

where:  $\bar{X}_a$  is the higher value of the two sample means,

$S_a$  its standard deviation,

$N_a$  the number of observations.

$tn_a \left( \frac{s_a}{\sqrt{N_a}} \right)$  the confidence limit for

the population mean with 95% probability ( $tn_a$  the value for  $t$  with  $n_a$  degrees of freedom),

$$\frac{(N_a - 1) s_a^2}{n_a \chi_{.975}^2} \text{ and } \frac{(N_a - 1) s_a^2}{n_a \chi_{.025}^2}$$

the lesser and greater values respectively of the 95% confidence limits of the variance ( $n_a$  degrees of freedom). See Simpson, Roe and Leewontin 1960, p. 161.

Similarly  $\bar{X}_b$  is the lower value of the two sample means, etc.

As mentioned above, taxonomists differ in the value of CD which they would require before recognizing distinct subspecies. In this connection, it would seem to be logical that the area below the curve of a population which the taxonomist should require to be free of overlap from another population should include the whole of the values which occur at greatest frequency, i.e., it should include that part of the curve within the range of 1 standard deviation on both sides of the mean; thus 84% of the population should be quite distinct. Ideally this should be distinct from the whole of any adjacent population but in practice it is probably sufficient that it should be overlap free from 97% of it (i.e., 2 standard deviations from its mean).

Thus, I would regard a population CD value of 1.5 as adequate to establish subspecies.

Procedure.—In order to test two samples for subspecific distinctness:

- Compare means of samples (t test) in all variates likely to give significance.
- For variates giving significant t values calculate  $CD_1$  and  $CD_2$ .

To interpret Results:

- If both  $CD_1$  and  $CD_2$  are 1.5 or greater the two populations warrant subspecific separation.
- If neither reaches 1.5 it is probable that the populations are not subspecifically distinct.

(c) If  $CD_1$  is less than 1.5 and  $CD_2$  is 1.5 or more then it is not possible with the material at hand to give subspecific recognition although further material might require it.

Comparison of *Thylacinus*.—In comparison between samples of modern *T. cynocephalus* and Western Cave-fossil *Thylacinus*, the observed means of the characters  $M^2$ ,  $M^3$ ,  $M^{1-4}$  were significantly different ( $P < 0.01$ ).  $CD$ ,  $CD_1$ , and  $CD_2$  were calculated for these and are given here.

	CD	$CD_1$	$CD_2$
$M^2$	1.21	0.48	2.23
$M^3$	1.04	0.32	2.10
$M^{1-4}$	0.93	0.16	2.15

In the character  $M_4$ , where the differences between the means approach significance at the 5% level,  $CD = 0.336$ ,  $CD_1$  is a negative quantity, and  $CD_2 = 1.28$ .

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